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Bulletin

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of the

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BULLETIN
OF THE
TORREY BOTANICAL CLUB

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The Structure and Development of the Apical Meristem in the Shoots of Taxodium distichum[1]

G. L. CROSS

(WITH 25 FIGURES AND PLATES 8 AND 9)

Renewed interest in meristem has been stimulated by the researches of Schüepp (1926), Helm (1932), Louis (1935), Foster (1935, 1938), Kaplan (1937), and many others. Much of the recent work has been done with angiosperms, but the papers of Korody (1937), Härtel (1938), and Foster (1938) have shown the need for comparative work in the more primitive groups. The present paper deals with apical meristem in the shoots of *Taxodium distichum* Rich. Interest in this species was stimulated by the dearth of literature concerning the morphology of its highly complex shoot system, and by the confused and conflicting reports regarding the structure of its shoot apex (Korschelt, 1884; Groom, 1885). Although emphasis here is placed on the structure of the apical meristem in expanding deciduous and permanent shoots, the origin of the shoot apex[2] of certain of the deciduous shoots is described briefly.

MATERIALS AND METHODS

Materials were collected from two trees growing on the campus of the university of Oklahoma, Norman, and from trees growing in the flood plain forests of southeastern Oklahoma (McCurtain County).[3] Collections on the campus were made every third day throughout the season of 1937 extending from March 1 to September 1. The materials were killed and fixed under reduced pressure in a solution of 5 per cent commercial formalin and 6 per cent glacial acetic acid made up in 70 per cent

[1] Contribution from the Botanical Laboratory, University of Oklahoma, No. 55.

[2] In an effort to secure uniformity in terminology, "shoot apex" will be used to designate the apical region of the axis (Foster, 1938, footnote 2).

[3] Collecting trips were financed in part by a University Research Grant.

[THE BULLETIN FOR JUNE (66: 341–429) WAS ISSUED JUNE 5, 1939]

ethyl alcohol. A series of tertiary butyl alcohols were used for dehydration and clearing, and the usual technique of embedding in paraffin (56° C.) was employed. Serial sections, longitudinal and transverse, were cut 8–10μ in thickness. Safranin and Fast Green F. C. F. were used in staining (Cross, 1937a).

The drawings were prepared with the aid of a camera lucida. A 4.3 mm. fluorite oil immersion objective and an 8× periplan ocular were used in making the photomicrographs, with the exception of Plate 8, figure 10, for which a 16 mm. apochromatic objective was used.

GENERAL FEATURES OF THE TWIGS

It is generally known that *Taxodium distichum* produces deciduous shoots which absciss and fall from the permanent twigs at the end of each season of growth (Henry, 1837; Coulter, 1889; Velenovský, 1905; Bernard, 1926; Doak, 1935), although apparently no description of the initiation and development of the deciduous shoots has appeared in the literature.

The general features of the twigs have been described in an earlier paper (Cross, 1939), in which four types of deciduous twigs, classified with respect to place of origin and time of expansion were listed, viz., those which arise exogenously in the axils of the upper scale-leaves of the expanding permanent twig, and expand with the parent twig; those which are formed "pseudo-endogenously" in the lower scale-leaves of the permanent twig, and expand one year later; those which arise endogenously near the base of the lower scale-leaves and scales of the permanent twig; and those which arise in the axils of the lower scales of pre-existing deciduous shoots.

A consideration of Plate 8, figures 1–6, should be of aid in understanding the shoots of *Taxodium*. Figure 1 shows an apparent terminal, but actually lateral, bud of a permanent twig. To the left in the illustration is a young megasporangiate strobilus. Another bud of a per-

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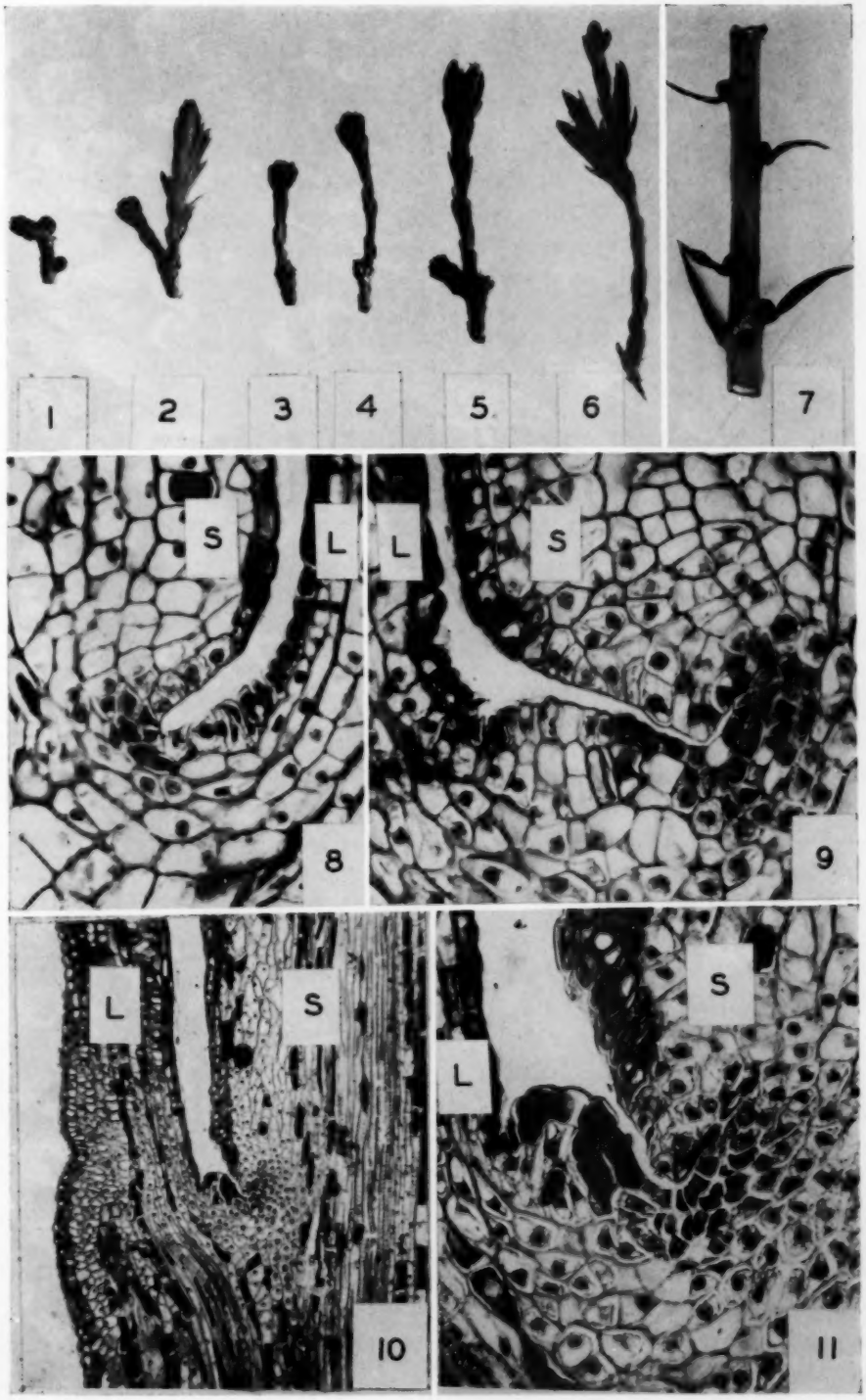
Explanation of Plate 8

All photographic work was done by William Felkner, Norman, Okla.

Figs. 1–6. A series illustrating the expansion of a permanent twig; explanation in text. ×1¼.

Fig. 7. Dormant buds of "pseudo-endogenous" axillary deciduous shoots showing splitting of the overlying cortical tissue. ×2.

Figs. 8–11. Longisections of primordia of buds of "pseudo-endogenous" deciduous shoots in various stages of development; *l*, leaf of parent shoot; *s*, stem of parent shoot. Figs. 8, 9, 11, ×220. Fig. 10, ×55.



CROSS: TAXODIUM

manent twig appears a short distance removed from the apex on the right side of the parent twig. Figure 2 illustrates the expansion of a bud of a permanent twig (to the left) and of a deciduous twig (to the right). Figures 3–6 show permanent twigs in various stages of expansion. Figures 5 and 6 show the expansion of exogenous axillary deciduous shoots from the distal portions of the permanent twigs. A twig the size of the one shown in figure 6 will have, in the axils of many of its proximal scale-leaves, the primordia of "pseudo-endogenous" deciduous shoots

Fig. 1. Diagram illustrating longisection of expanding permanent shoot with buds of axillary deciduous twigs; *a*, apical meristem; *exb*, primordia of buds of exogenous deciduous shoots; *enb*, primordia of buds of "pseudo-endogenous" deciduous shoots.

(Cross, 1939), but these, in contrast to the exogenous shoots, do not expand at the same time that the permanent twig expands. Their expansion is delayed until the following spring and, in some cases, longer.

THE INITIATION OF THE "PSEUDO-ENDOGENOUS" BUDS

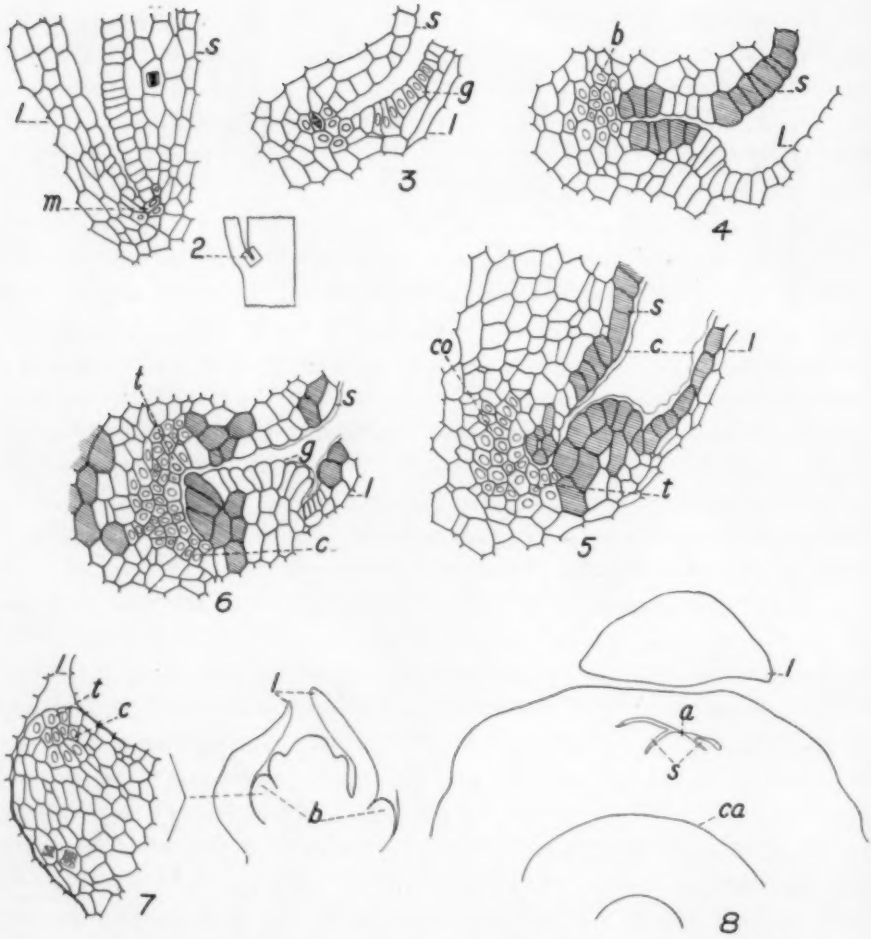
A diagram of a longitudinal section of a permanent twig showing the location of primordia of the two types of axillary deciduous shoots is shown in figure 1. In the axils of three of the more distally placed leaves are the primordia of exogenous deciduous shoots. The deciduous shoots

are formed early in the spring—in some cases before the expansion of the parent bud. They expand at the same time that the parent bud expands, and they abscise in the fall following their expansion. Thus initiation, expansion, and abscission usually occur during the same growing season. The exogenous deciduous shoots (fig. 7) present no unusual features of initiation or developement.

In the axils of two of the proximal leaves in figure 1 may be seen the primordia of deciduous shoots, which for convenience in making distinctions, have been termed "pseudo-endogenous." The initiation of these buds is delayed, in most cases apparently until the first two weeks in June, although the time of their formation varies somewhat with their distance from the apex of the permanent shoot. They develop during the summer, are dormant during the autumn and ensuing winter (Plate 8, fig. 7), and finally expand the next spring—one year after the parent twig has expanded and nearly one year after the neighboring exogenous buds have expanded. In contrast to the exogenous buds, the "pseudo-endogenous" buds are initiated the first year, but expand and abscise the second year.

"Pseudo-endogenous" buds are formed in the axils of many, but not all, of the proximal leaves. One of the first indications of their initiation is the periclinal division and enlargement of the cells of the cortex immediately above the axil of the leaf (fig. 2). As a result of these cellular divisions the cortex enlarges and crowds the leaf outward, leaving a narrow axillary slit in the bottom of which the apical meristem of the bud will be initiated (figs. 3–6; Plate 8, figs. 8–11). The division and enlargement of the cells of the cortex is usually accompanied or succeeded by a distinctive behavior of an area of the cells on the adaxial surface of the subtending leaf (fig. 3; Plate 8, fig. 8). These cells usually elongate considerably in a plane perpendicular to the surface of the leaf and form a glandular appearing mass, the surface of which is frequently elevated by periclinal and oblique divisions of the constituent cells. The elevated portion becomes closely appressed to the epidermis of the permanent shoot (figs. 4–6).

The cells of the epidermis and cortex below the bottom of the axillary slit remain meristematic (figs. 2, 3) during the developmental stages just described. Their protoplasts stain densely and dividing cells are easily demonstrated (fig. 3; Plate 8, fig. 8). At this stage, nearly median sections show that the epidermal cells in the bottom of the slit undergo repeated anticlinal divisions. The derivatives of these divisions become the tunica of the young bud (figs. 5, 6). It is shown later that the tunica



Figs. 2–6. Median longisections through axils of leaves, showing origin of apical meristem of "pseudo-endogenous" deciduous shoot; *l*, leaf; *s*, stem; *m*, meristematic cells; *g*, glandular cells; *b*, primordium of bud; *t*, tunica; *co*, corpus; *c*, cuticle. ×165.

Fig. 7. Nearly median longisection of apical meristem of young exogenous deciduous shoot. ×165.

Fig. 8. Transection above node of permanent shoot showing embedded "pseudo-endogenous" bud of deciduous twig; *ca*, cambium. ×41.

usually maintains its identity until the bud becomes dormant. During the initiation of the tunica certain epidermal cells on the axis, above the young bud, and on the adaxial surface of the subtending leaf, become filled with a densely staining material. Such cells are indicated by hatching (figs. 4–6).

The cells of the tunica then enlarge periclinally, thus increasing the surface area of the apical meristem and widening the bottom of the axillary slit. However, concomitant enlargement of the cells in the stem and in the subtending leaf keep the slit from opening, and the epidermal cells belonging to the portion of the stem immediately above the young axillary bud are soon seen to extend as a lobe down over the bud (figs. 5, 6). During these developmental phenomena, increased mitotic activity in the cells immediately below the tunica results in the initiation of a corpus (figs. 5, 6). The rapidly enlarging lobe of the parent stem above the bud and the continued growth of the glandular mass on the adaxial surface of the subtending leaf sometimes results in an overlapping of these structures (fig. 5). More frequently the upgrowth from the leaf is more vigorous and dominates the lobe from the stem so that the latter is flattened and pressed upward (fig. 6).

When the surface area of the young bud has reached an extent approximately equal to that indicated in figure 6, the first foliar appendages are formed. These consist of two fleshy scales which arise almost simultaneously, nearly opposite each other, in a plane approximately perpendicular to the axis of the permanent twig. Transections prepared at this stage are often confusing for they give the false impression that the bud is endogenous (fig. 8). Details concerning the origin of the scales or of the immediately succeeding foliar structures were not obtained. However, it may be well to remind the reader that abscission of the deciduous shoot will ultimately occur in a plane above the first scales (Doak, 1935; Cross, 1939) and that buds of deciduous shoots will finally be formed in the axils of one or more of the scales.

The development and emergence of the bud from its sunken position in the axillary slit was observed. As the bud increases in size there is much cracking and uplifting of the overlying portions of the stem and leaf (Plate 8, fig. 7).

GROWTH AT THE APEX OF THE SHOOTS

Apparently the earliest recorded work on the structure of the apical meristem of *Taxodium* is that of Korschelt (1884), who described and prepared illustrations of surface and longitudinal views of the shoot apex of *T. distichum*. Korschelt interpreted apical growth as occurring through the activity of a single tetrahedral apical cell, similar in many respects to apical cells found in cryptogams. Groom (1885), working with the apices of "strongly growing lateral shoots" of *T. distichum*, described: (1) a sharply delimited dermatogen in which he never observed periclinal

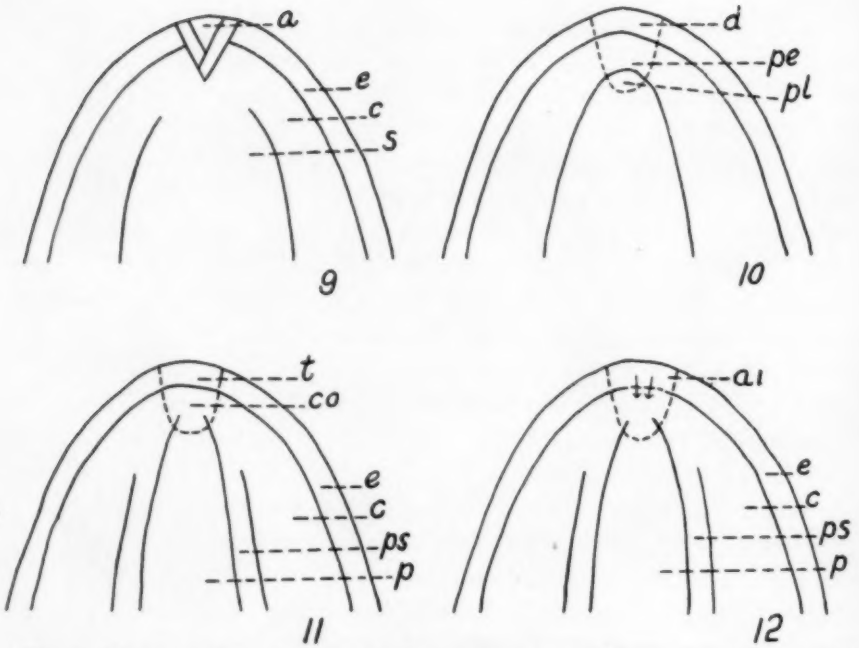


Fig. 9. Diagram of longisection of shoot apex prepared from Korschelt's (1884) description; *a*, apical cell; *e*, epidermis; *c*, cortex; *s*, stem.

Fig. 10. Diagram of longisection of shoot apex prepared from Groom's (1885) description; *d*, dermatogen; *pe*, periblem; *pl*, plerome.

Fig. 11. Diagram illustrating structure of shoot apex of permanent and some deciduous shoots as seen in longisection; *t*, tunica; *co*, corpus; *e*, epidermis; *c*, cortex; *ps*, provascular strand; *p*, pith.

Fig. 12. Diagram illustrating structure of shoot apex of certain deciduous shoots as seen in longisection; *ai*, periclinally dividing apical initials indicating lack of distinction between tunica and corpus.

divisions; (2) a somewhat irregular periblem; and (3) a plerome dominated by 1–3 initial cells. Groom did not specify whether he worked with permanent or with deciduous twigs. In general his results are in agreement with the earlier work of Strasburger (1872) who made a comprehensive study of the stem apices in several groups of gymnosperms. However, Strasburger recognized that irregularities in the behavior of the dermatogen, periblem, and plerome are likely to occur. According to Karsten (1886) the stem apex of the seedling of *T. distichum* possesess a distinct plerome terminated by a single initial, a periblem, and a dermatogen which exists as a continuous layer but is not genetically independent of the periblem. The interesting differences of opinion developed by Korschelt (1884) and Groom (1885) concerning the structure of the shoot apex of *Taxodium* obviously are worthy of reinvestigation.

Perhaps at the outset, the fact should be emphasized that the structure of the shoot apex as described in this paper is not in accord with the earlier reports (Korschelt, 1884; Groom, 1885). The differences can best be understood by reference to figures 9–12. Figure 9 is a diagram which illustrates the type of apical growth as interpreted by Korschelt (1884) for *Taxodium*. The entire shoot is here referred in origin to the activity of a tetrahedral apical cell. The opposing view, developed by Groom (1885), is represented in figure 10, where the shoot is depicted as arising through the activity of three discrete histogens—the dermatogen, periblem, and plerome. The interpretations suggested in the present paper are summarized in figures 11 and 12. Figure 11 illustrates a condition which seems to be fairly constant for permanent shoots, although it was found in less than one-half of the deciduous shoots. In contrast to Groom's account, the periblem and plerome are not distinguishable as separate histogens at the shoot apex and the entire apical meristem is equivalent to an angiospermous shoot apex of the type possessing a one-layered tunica and a central corpus. Figure 12 represents a condition which seems to occur frequently in deciduous shoots but infrequently, or perhaps never, in the permanent twigs. In this type of apex the identity of the tunica is lost or is not maintained constantly. Periclinal divisions occur in the outer layer at or near the apex and the internal derivatives augment the underlying meristematic mass. This condition approaches that described for many gymnosperms (Strasburger, 1872; Koch, 1891; Korody, 1937; Foster, 1938). The significance of this variable apical growth (figs. 11, 12) is discussed later.

The shoot apex of *T. distichum* is circular in transection. The average diameter of fifty apices, taken at a plane equidistant from the apex and the top of the youngest foliar primordium, is 140μ in deciduous shoots and 170μ in permanent shoots. Measurements of various deciduous shoots did not reveal any constant difference in size. The longitudinal configurations of the apices of deciduous and permanent twigs are illustrated in figures 13–22. The average height of the shoot apex measuring from the tip of the axis to the upper surface of the youngest foliar primordium was about 100μ in the deciduous shoots and 80μ in the permanent shoots.

THE SURFACE LAYER OF THE APICAL MERISTEM

As stated earlier, the stem apices of the axillary deciduous shoots are characterized by an early differentiation of a peripheral tunica and central corpus (figs. 6, 7). That this is true of the exogenous deciduous

shoots as well as of the endogenous ones has been confirmed by a careful study of numerous buds in the primordial stage. Observations of a limited number of very young buds of permanent shoots indicate that they possess an organization similar in most details to that found in the primordia of exogenous deciduous shoots (fig. 7). Thus a similar basic architecture (tunica and corpus) is found in the shoot apices of all primordial buds on the permanent twigs of *Taxodium*. An investigation of the axillary buds which develop on deciduous shoots has not been made. The identity of the tunica and corpus apparently is maintained in all resting buds. The condition of the apical meristem of a dormant bud of a "pseudo-endogenous" deciduous shoot is shown in figure 13. Here the one-layered tunica (delimited by a heavy line in the illustration) appears as a distinct layer over the somewhat massive corpus. Examination of a large number of resting buds has failed to reveal evidence of any but anticlinal divisions in the tunica. However, during shoot expansion, considerable variation in structure of the shoot apex can be demonstrated. Over fifty deciduous shoots were sectioned for study and of these, approximately one-half were found to have well organized tunicas agreeing closely in most features with those depicted in figures 14 and 16. No indication of an apical cell, as described by Korschelt (1884) was found in any of the sections. Occasionally groups of conspicuously large cells were found at the apex (Plate 9, fig. 1). Studies of transections revealed that these rather large apical initials occur in groups of three or four; they are similar in size, and are characterized by somewhat greater mitotic activity (fig. 15). It seems apparent that apices of the type shown in figures 14 and 16 are essentially equivalent to those present in certain angiosperms such as *Scrophularia nodosa* L., where a one-layered tunica has been reported (Schmidt, 1924).

In slightly less than 50 per cent of the deciduous shoots examined, periclinal divisions in the cells of the surface layer of each shoot apex had interrupted the continuity of the tunica (figs. 17, 18; Plate 9, fig. 2). The divisions seem to vary considerably with respect to the location and extent of their occurrence. In figure 17 a cell of the surface layer to the left of the apex has divided periclinally and the outer derivative has divided anticlinally. Elsewhere at the apex an easily delimited dermatogen is present. Although decisive evidence could not be obtained it seems reasonable to assume that in many cases the continuity of the dermatogen is only occasionally interrupted by such periclinal divisions and that this outer layer is again organized after each periclinal division. Thus

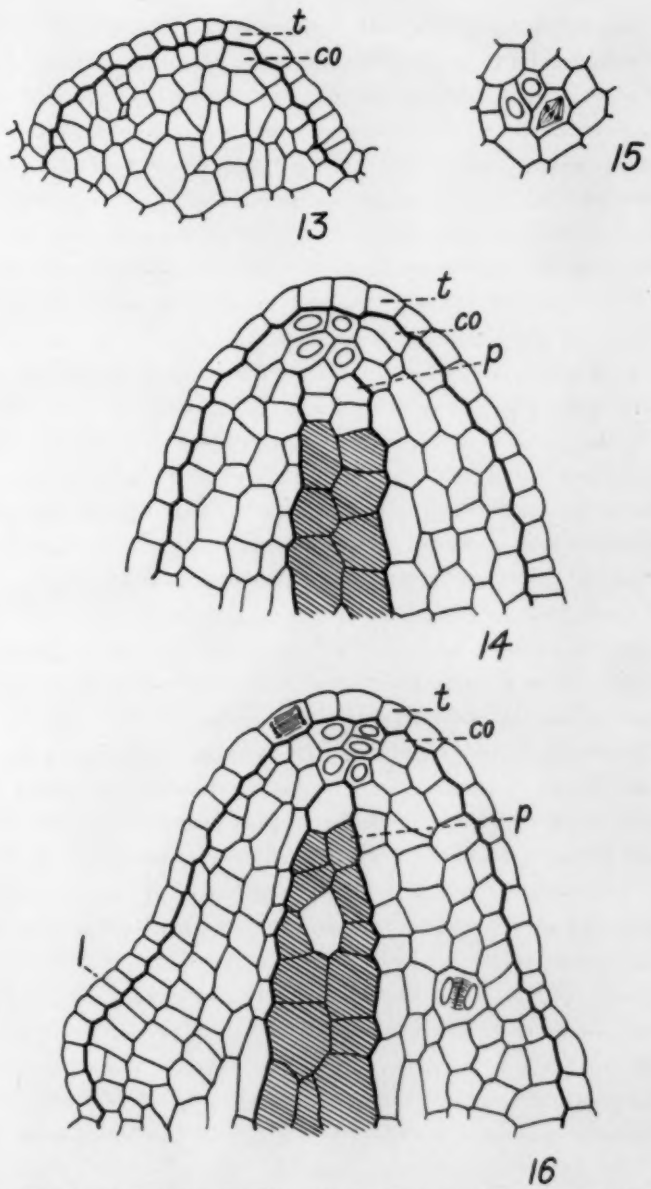


Fig. 13. Nearly median longisection of shoot apex of dormant bud of deciduous shoot; *t*, tunica; *co*, corpus. ×330.

Fig. 14. Median longisection of shoot apex of expanding "pseudo-endogenous" deciduous shoot; *p*, pith initial. ×330.

Fig. 15. Surface view of apex of deciduous shoot. ×330.

Fig. 16. Median longisection of shoot apex of expanding exogenous deciduous shoot; *l*, primordium of leaf. ×330.

an apex with apparently discrete histogens might have occasional periclinally dividing cells in the surface layer. A statistical study based upon the observation of a large number of deciduous shoots should yield valuable data. Figure 18 indicates that in certain deciduous shoots periclinal divisions may occur extensively in the surface layer of the shoot apex. The cell-complex at the tip of this shoot has clearly arisen either from two successive periclinal divisions of a pair of surface cells, or from the periclinal and anticlinal divisions of a single cell. The internal derivatives of these divisions augment the corpus. A similar condition is shown in Plate 2, figure 2. This condition is suggestive of the apical initial group described by Foster (1938) for *Ginkgo biloba*. However, in contrast to *Ginkgo*, and many other conifers (Koch, 1891; Korody, 1937), periclinal divisions in the surface layer of the stem apex of *Taxodium* are confined to the apical portion of the meristem. Only anticlinal divisions occur in the lateral portions of the surface layer; in this respect the shoot apex of *Taxodium* may be regarded as more highly organized than that of the other genera; it is transitional between the condition which obtains in *Pinus* and in certain angiosperms.

Longitudinal sections of twelve permanent shoots were compared with the sections of the deciduous shoots. The evidence appears conclusive that the prevailing condition in the shoot apex of the permanent twigs is characterized by a well organized tunica (fig. 22; Plate 9, fig. 3). Evidence of periclinal divisions could be found in only one shoot (fig. 21) and here the interpretation is open to doubt. However, in the light of the information obtained from the deciduous shoots, it would not be surprising if periclinal divisions were found to occur infrequently in the apical surface layers of permanent shoots. It should be mentioned that the interpretation of the apex shown in figure 22 agrees in part with the description by Groom (1885), except that Groom reported a distinct periblem and plerome. It is probable that Groom worked with expanding permanent shoots.

The apices of several proliferating shoots, which seemed to be intermediate with respect to external form (Cross, 1939) between typically deciduous and permanent shoots, were studied. The results indicate that these shoots have apical meristems essentially similar to those of the permanent shoots (figs. 19, 20).

In summary, three distinctive types of shoot apex, with respect to the structure of the surface layer, were found in *Taxodium*, viz., apices which possess a highly organized tunica—found in permanent shoots, inter-

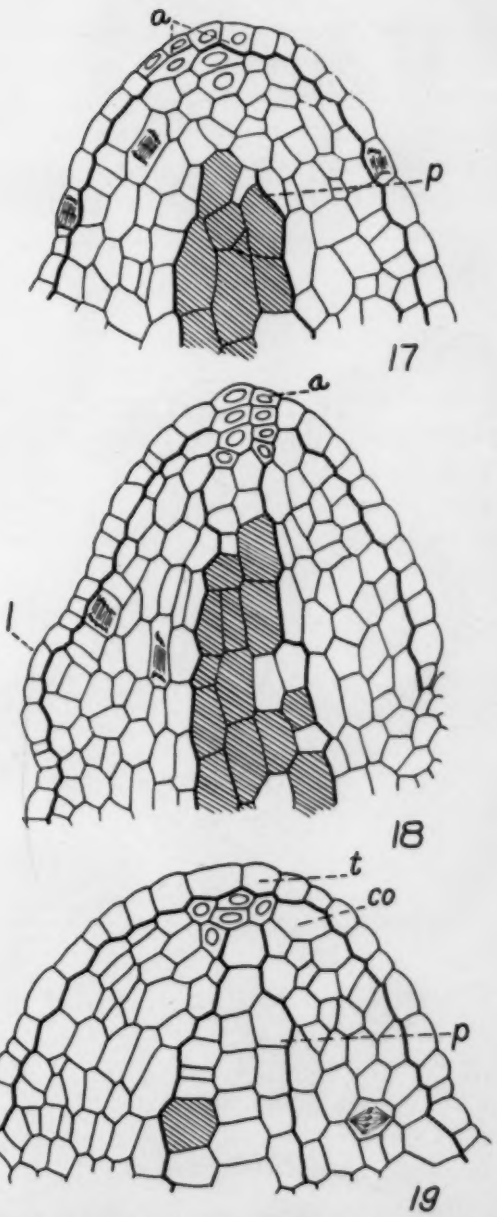


Fig. 17. Nearly median section of shoot apex of expanding deciduous shoot; *a*, apical initials; *p*, pith initials. ×330.

Fig. 18. Median section of shoot apex of expanding deciduous shoot; *a*, apical initials; l, primordium of leaf. ×330.

Fig. 19. Nearly median longisection of shoot apex of transitional proliferating shoot. ×330.

mediate shoots, and many deciduous shoots; apices in which the continuity of the tunica is interrupted temporarily by occasional periclinal divisions —found in many deciduous shoots and possibly occasionally in permanent ones; and apices in which the continuity of the surface layer is more or less permanently interrupted by a mass of periclinally and anticlinally dividing, genetically related cells—found infrequently in deciduous shoots. These types are connected by many intergrading forms.

THE SUBAPICAL PORTION OF THE SHOOT APEX

The subapical portion of the shoot apex consists in part of a zone of central embryonic cells equivalent in position, but not in structure, to the "central mother cells" of *Ginkgo* (Foster, 1938). The subapical initials, unlike the surface cells, have a relatively uniform structure in the various shoots (figs. 13–22; Plate 2, figs. 1–3). In the deciduous shoots there are 4–8 subapical initials arranged as a cap over the initials of the pith (figs. 14, 16, 18; Plate 9, fig. 1). As a result of periclinal and anticlinal divisions, derivatives are produced which augment the pith initials and contribute laterally to the flanks of the apex respectively. The procedure probably is reduced to its simplest terms in Plate 2, figure 1, where recent subapical activity can be traced with reasonable certainty. In the apex, immediately beneath the tunica in this illustration is a group of four cells consisting of a large pith initial and three overlying smaller cells. It seems evident that these four cells constitute a genetically related group which has developed from a single mother cell by the insertion of three walls. The flanks of the corpus diverge laterally from the three smaller cells of this genetic group and ultimately differentiate into the procambial and cortical regions of the shoot. In deciduous shoots which lack a tunica (figs. 17, 18), essentially the same situation obtains with respect to the subapical initials except that the divisions tend to be somewhat oblique.

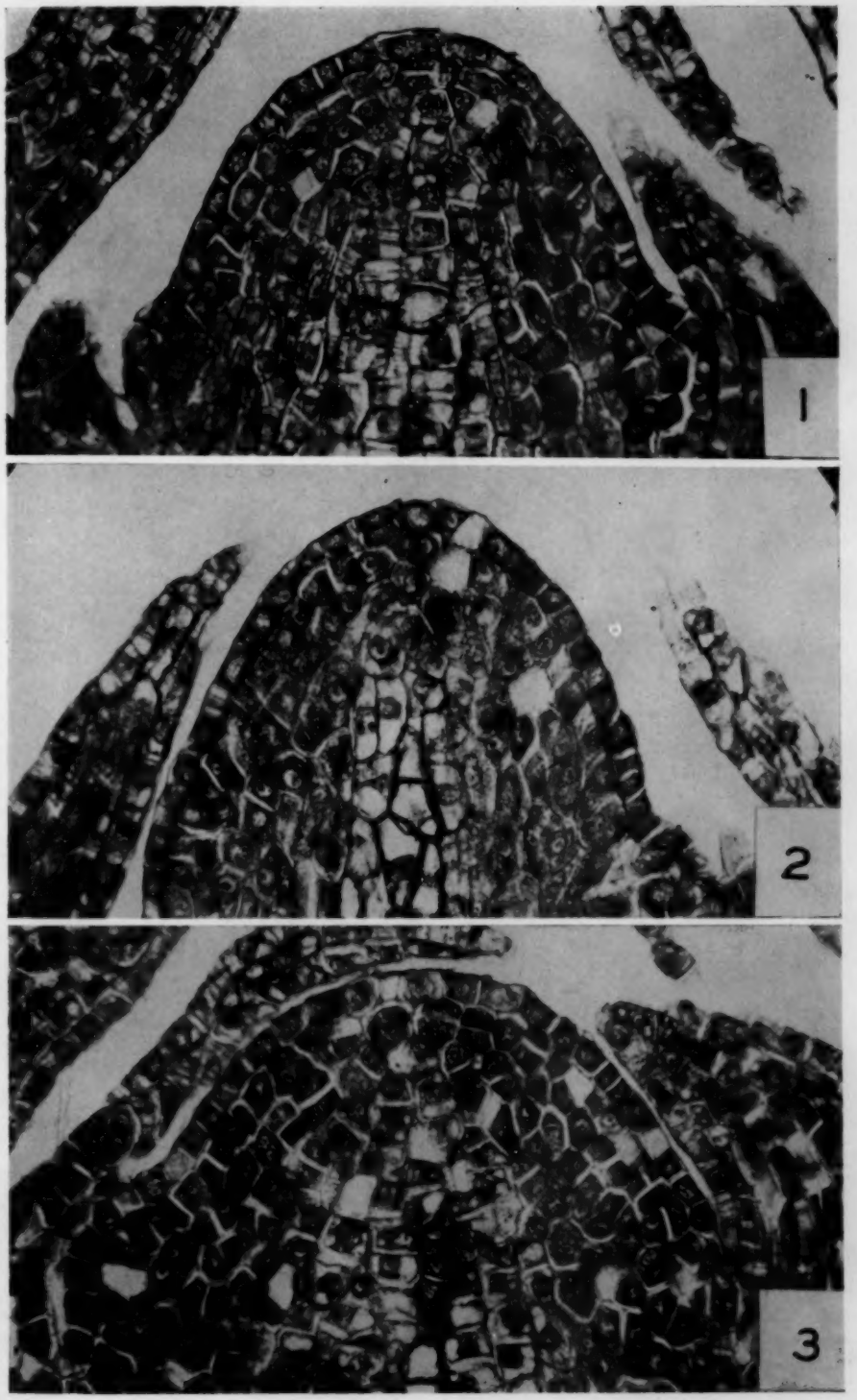
The subapical initials of the permanent shoots are arranged in several tiers, thus giving a more massive appearance to the apical meristem (fig.

Explanation of Plate 9

Fig. 1. Longisection of shoot apex of expanding deciduous shoot showing a clearly delimited tunica and corpus. ×330.

Fig. 2. Longisection of shoot apex of an expanding deciduous shoot showing a group of apical initials in one of which a periclinal wall has been inserted. ×330.

Fig. 3. Median longisection of shoot apex of an expanding permanent shoot showing a clearly delimited tunica and corpus—a prevailing condition in permanent shoots. ×330.



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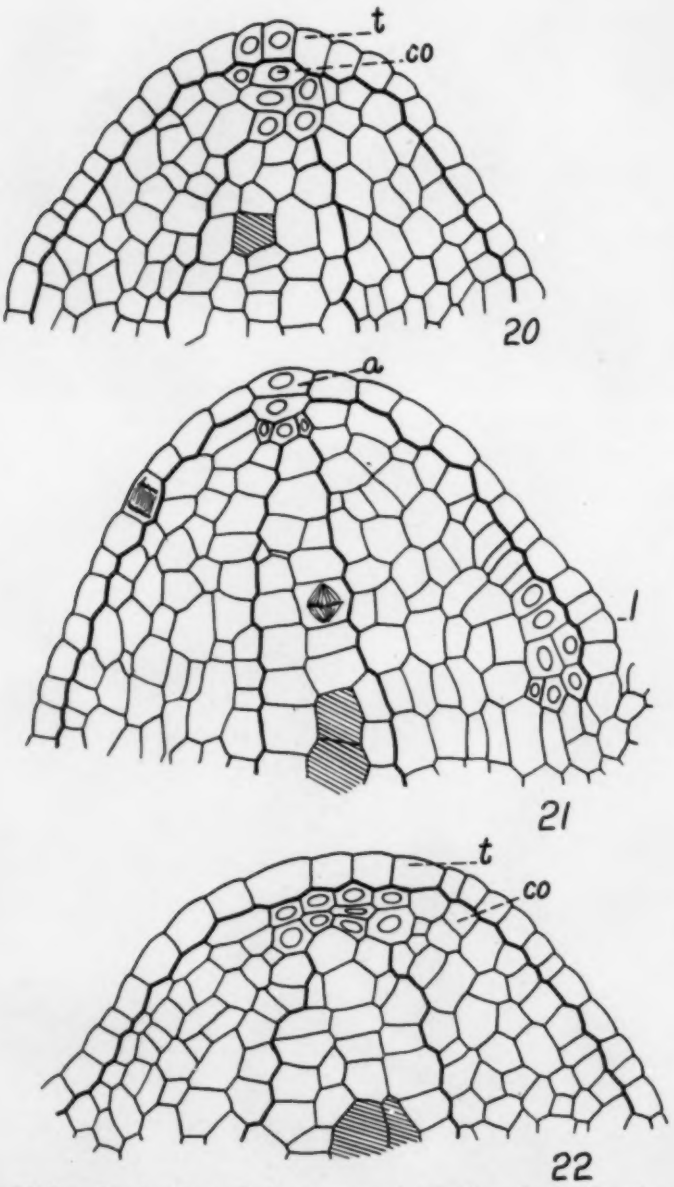


Fig. 20. Median longisection of shoot apex of transitional proliferating shoot; *t*, tunica; co, corpus. ×330.

Fig. 21. Nearly median longisection of shoot apex of expanding permanent shoot showing evidence of periclinal division in the tunica; *a*, apical initial; *l*, primordium of leaf. ×330.

Fig. 22. Median longisection of shoot apex of expanding permanent shoot illustrating prevailing condition. ×330.

22; plate 9, fig. 3). The initials divide anticlinally as well as periclinally and are similar in other respects to the subapices of the deciduous shoots.

The pith is delimited arbitrarily by a heavy line in the illustrations (figs. 14–22). The line is necessarily arbitrary because of the vague lateral limits of the older portions of the pith (Plate 9, figs. 1–3). The initials of the pith frequently extend to within two cells of the surface layer (figs. 14, 16, 18, 19; Plate 9, fig. 1). They form a "rib meristem" (Schüepp, 1926) which is continuously augmented from above by periclinal divisions in the subapical initials. The cells of the young pith are of the typically highly vacuolated type (Plate 2, figs. 1–3), common in the stem apices of many conifers (Koch, 1891; Korody, 1937).

Certain of the pith cells have densely staining materials deposited in their protoplasts, particularly in the peripheral cytoplasm. The central vacuole and the nucleus usually remain free of such deposits (Plate 9, figs. 1–3) and mitotic activity is in no way inhibited. The densely-staining cells are indicated by hatching in the text figures.

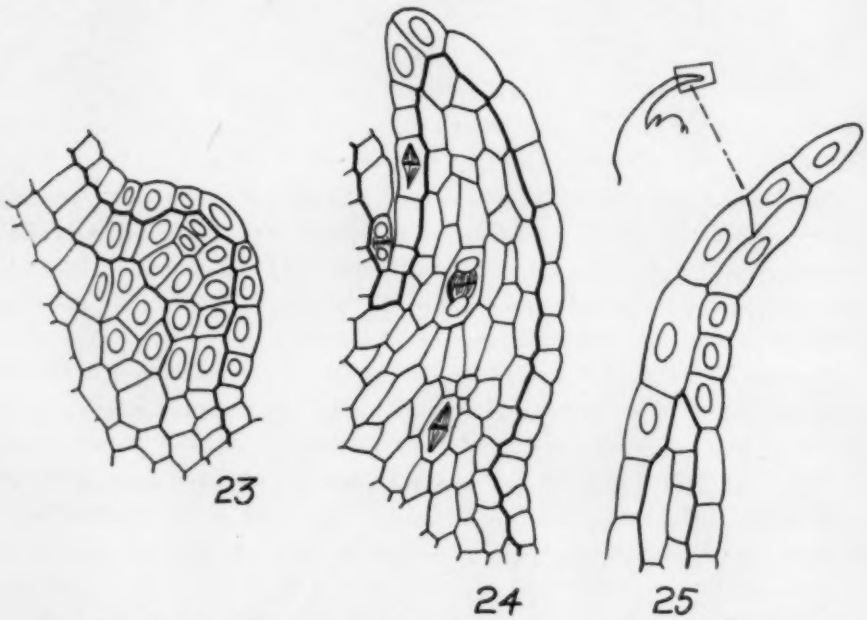
It seems evident that the subapical portion of the stem apex of *Taxodium* consists of three regions characterized by the position, size, staining reaction, and mode of division of the constituent cells, viz., the central initials; the pith initials; and the meristematic flanks, derivatives of which differentiate into procambial and cortical tissue. It further seems evident that the angiospermous condition is attained by the permanent shoots and many of the deciduous shoots of *Taxodium;* the only significant difference is that, in many angiosperms, the pith initials are differentiated at a considerably greater distance from the shoot apex (Foster, 1935; Cross, 1936, 1937b).

ORIGIN OF LEAVES

In many primitive vascular plants which lack a differentiated surface layer at the shoot apex, leaf initiation is characterized by periclinal divisions in the epidermal layer as well as in the subepidermal layers. This type of leaf initiation occurs in *Abies, Picea, Pinus* (Korody, 1937), *Lycopodium* (Härtel, 1938), and in various other gymnosperms (Strasburger, 1872). In many angiosperms (Foster, 1935; Cross, 1937b, 1938) periclinal divisions do not occur in the tunica during foliar initiation. Because *Taxodium* is regarded in this paper as being intermediate with respect to its apical meristem between the condition obtaining in primitive vascular plants and that expressed by angiosperms, it was thought ex-

pedient to include a brief description of the initiation of the leaf, with emphasis on the behavior of the epidermal layer.

Many median or nearly median sections of leaves in various stages of development were seen during the study. Leaves are initiated approximately 100μ in deciduous shoots and 80μ in permanent shoots below the shoot apex. Preliminary stages in leaf initiation involve an elongation of



Figs. 23, 24. Median longisections of young leaves showing contributions of epidermis and subepidermal layers during initiation. ×330.

Fig. 25. Median longisection of young leaf 350μ high showing derivation of apical portion from epidermal cells. ×330.

the cells of the subepidermal layer in a plane perpendicular to the surface of the stem. One or more of the subepidermal cells usually divides periclinally during or after elongation (figs. 16, 18, 21). Periclinal divisions were never observed in the epidermal layer, a fact which is in agreement with Karsten's (1886) brief account of foliar initiation in the seedling. Further periclinal divisions, apparently largely in the derivatives of the subepidermal layer (fig. 23), increase the size of the primordium. The epidermal layer maintains its identity and shows no indication of periclinal divisions until a height of approximately 110μ has been attained, measuring along the adaxial surface. At this stage two epidermal cells, conspicuous because of their size and distinctive shape, may be seen in

longitudinal section at the apex of the young leaf (fig. 24). These two cells maintain their identity without dividing until the leaf is nearly 150μ high. They then divide in such a manner as to form two vertical adjacent rows of cells (fig. 25). The derivatives divide anticlinally, parallel with the longitudinal axis of the leaf, and form a triangular apex two cells in thickness. Ultimately, one of the pair of dividing apical cells, usually the abaxial one, grows beyond the other (fig. 25) and forms a single-celled apex. Thus the epidermal layer contributes nothing during initiation to the internal portions of the leaf and contributes only sparingly during the later growth of the leaf.

DISCUSSION

It has been suggested by Korody (1937) and Härtel (1938) that the entire apical meristem in certain of the more primitive vascular plants is homologous with the corpus in angiosperms. This viewpoint has been criticized by Foster (1938) who regards the tunica and corpus as interdependent growth zones. In some of the deciduous shoots of *Taxodium distichum* apical meristems are found which are comparable in structure to those reported by Korody (1937) for *Abies*, *Picea*, and *Pinus*. According to Korody's interpretation, the apex of each of these deciduous shoots would consist of a corpus without a tunica. Other deciduous shoots of *Taxodium* seem to have meristems in which an incipient tunica is present. In such cases the continuity of the primitive tunica is interrupted more or less frequently by the insertion of periclinal walls, but the presence of a semi-independent surface layer is not to be doubted. Still other deciduous shoots, and probably all permanent shoots, have a tunica and corpus existing as constantly discrete histogens. Many shoot apices transitional between these three types were seen. Additional study would doubtless reveal that a much closer series could be demonstrated than that shown in figures 14–22. Again applying the principles adduced by Korody, one is forced to homologize the corpus of the permanent shoots with the entire apical meristem of certain of the deciduous shoots. Further, the corpus of one group of deciduous shoots would be homologous with the entire apical meristem of other deciduous shoots located on the same tree. In other words, the tunica, according to Korody, is a phylogenetic derivative of the corpus. The validity of such reasoning depends upon the meanings arbitrarily assigned to the words "tunica" and "corpus." As originally introduced by Schmidt (1924) these terms were used to describe differentiation in the form of zonation at the shoot apex. In my opinion

the application of Korody's interpretation does not lead to a greater understanding of the fundamental morphology of the shoot apex in vascular plants. It seems more reasonable to assume that the relatively undifferentiated shoot apex found in many gymnosperms is equivalent to the entire angiospermous shoot apex—that the tunica and corpus appear simultaneously as a result of phylogenetic zonation.

From a single branch of *Taxodium*, an evolutionary series can be arranged showing shoot apices of varying degrees of evolutionary advancement. It is of course difficult to determine in which direction the series should be read, but there is a temptation to regard as primitive those apices with undifferentiated histogens. This seems logical, especially in the light of information obtained from the study of other relatively primitive vascular plants (Korody, 1937; Härtel, 1938; Foster, 1938). Foster (1938) regards "the condition in the Abietaceae as indicative of a transitional stage in the evolution of the zonation typical of the shoot tip in angiosperms." He further suggests that "the structural pattern in *Ginkgo*" may be more primitive than the condition in the Abietaceae. It seems reasonable to interpret the condition in the deciduous twigs of *Taxodium* as more advanced than in the Abietaceae, because in this genus periclinal divisions in the surface layer of the shoot apex are restricted to the apical cells; the cells in the surface layer on the flanks of the shoot apex divide only anticlinally. The permanent shoot of *Taxodium*, with its morphologically independent tunica and corpus, may be regarded as having attained the angiospermous condition.

SUMMARY

The shoot apices of the axillary deciduous shoots and permanent shoots of *Taxodium distichum* are described. In the primordial condition the apical meristems of all shoots investigated are characterized by a clearly delimited tunica and a central corpus. This condition persists during the expansion of most of the permanent shoots and a large proportion of the deciduous shoots. Occasional periclinal divisions occur in the surface layer at the shoot apex of many deciduous shoots. In other deciduous shoots periclinal divisions in the surface layer at the shoot apex occur so frequently that the continuity of the outer layer is completely interrupted by a zone of apical initials. Derivatives of the apical initials augment the subapical portion of the apex.

The subapical portion of the shoot apex in both types of shoots consists of three meristematic regions, i.e., the subapical initials; the

meristematic flanks; and the pith initials. The subapical initials located immediately below the apex constitute a focus of meristematic activity from which the other meristematic regions diverge. The pith initials, located immediately below the subapical initials, form a "rib meristem," derivatives of which mature into pith cells. The meristematic flanks diverge laterally from the subapical initials. Derivatives of this region ultimately differentiate into the cortical and procambial tissues of the axis of the shoot.

The primordia of leaves are initiated by the radial elongation and periclinal divisions of the outer layer of the corpus. The surface layer (tunica) does not contribute to the internal tissues of the primordia during initiation.

It is suggested that the shoot apices of the various shoots of *Taxodium* constitute a developmental series which might be useful in understanding the evolution of the highly organized angiospermous apical meristem. In this series it has seemed logical to interpret as most primitive those deciduous shoots in which a group of apical initials interrupts the continuity of the tunica. This type of shoot apex is regarded as slightly more advanced than the apices of many other conifers (Koch, 1891; Korody, 1937) because periclinal divisions in the surface layer are restricted to the apex and do not extend to the flanks of the shoot tip.

The data obtained from this study do not support the theory that the shoot apex in many primitive vascular plants is homologous with the corpus in angiosperms (Korody, 1937; Härtel, 1938).

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Additions to the Flora of the Glacier Bay National Monument, Alaska, 1935-1936

WILLIAM S. COOPER

COLLECTIONS BY W. S. COOPER, 1935

In 1931 I published in this journal a list of the seed-plants and ferns of the Glacier Bay National Monument, Alaska,[1] based on collections made in the course of three expeditions, in 1916, 1921, and 1929. A few species collected by others at various times were included. A fourth expedition took place in 1935, in collaboration with Mr. W. O. Field, Jr., during which additional collections were made; to the previous total of 232 species, 31 have been added.

The glacial history of the region, necessary to an understanding of the vegetational features, has been presented in a recent paper.[2] A brief outline of my ecological studies is provided in the paper in this journal noted above, and detailed discussion will be found in three previous publications.[3] The ecological results of the 1935 expedition are embodied in a paper just issued.[4]

The additional species collected in 1935 are listed below, with the stations where found,[5] and notes as to habitat.

Equisetum fluviatile L. Bog on foreland (57).

Agrostis exarata Trin. Pioneer. Johns Hopkins Fiord.

Calamagrostis canadensis (Michx.) Beauv. Bog meadow on foreland (57).

Deschampsia caespitosa (L.) Beauv. Beach meadow on foreland (53).

Festuca ovina brachyphylla (Schult.) Piper. Pioneer (26).

Carex aquatilis Wahl. Bog meadow on foreland (57).

Carex aurea Nutt. Pioneer on wet gravel (54).

Carex brunnescens Poir. Bog meadow on foreland (57).

Carex leptalea Wahl. Bog meadow on foreland (57).

Carex limosa L. Bog on foreland (56, 57).

Carex pyrenaica Wahl. Bare sandy outwash on foreland (57).

Carex rostrata Stokes. Bog meadow on foreland (57).

[1] The seed-plants and ferns of the Glacier Bay National Monument, Alaska, Bull. Torrey Bot. Club, 57: 327–338. 1931.

[2] Cooper, William S. The problem of Glacier Bay, Alaska: a study of glacier variations. Geogr. Rev., 27: 37–62. 1937.

[3] Cooper, William S. The recent ecological history of Glacier Bay, Alaska, Ecology, 4: 93–128, 223–246, 355–365. 1923.

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[4] A fourth expedition to Glacier Bay, Alaska, Ecology, 20: 130–155. 1939.

[5] For locations of stations see Ecology, 12, p. 62, fig. 1, and Ecology, 20, p. 131, fig. 1.

Carex spectabilis Dewey. Bog on foreland (56).
Carex viridula Michx. Bog meadow on foreland (57).
Eriophorum chamissonis Mey. Pioneer at edge of pond (54); bog on foreland (56).
Juncus arcticus Willd. Wet-ground pioneer (26); bog meadow on foreland (57).
Goodyera decipiens Hook. Young climax forest on foreland (57).
Rumex occidentalis Wats. Bog on foreland (56).
Ranunculus cymbalaria Pursh. Gravel shore (26).
Ranunculus repens L. Beach meadow on foreland (53).
Arabis lyrata L. Pioneer on gravel (26, 27, 54).
Drosera rotundifolia L. Bog on foreland (57).
Parnassia parviflora DC. Wet-ground pioneer (26). This collection is in habit exactly like *P. kotzebuei* Cham., which is common in the region. In floral characters, however, it corresponds closely with *P. parviflora*, not previously reported.
Saxifraga bronchialis L. Pioneer on gravel (26).
Lathyrus palustris L. Beach meadow on foreland (53).
Epilobium palustre L. Bog on foreland (56, 57).
Vaccinium oxycoccus L. Bog meadow on foreland (57).
Gentiana humilis Stev. Beach meadow on foreland (53).
Nephrophyllidium crista-galli (Menzies) Gilg. Bog on foreland (56).
Mimulus langsdorfii Donn. Stream bank on foreland. Bartlett Cove.
Taraxacum officinale Weber. Edge of alder thicket on foreland (56).

Of these 32 species added to the flora, 25 were found on the foreland east of the mouth of the bay, which is composed of glacial and glaciofluvial material associated with the recent ice maximum of 150 to 200 years ago. In 1935 for the first time a serious attempt was made to investigate the flora and vegetation of this area. Since it is close to regions long undisturbed by glaciation, the list is naturally far more extensive than that of the shores recently vacated by the ice. Particularly noteworthy is the rich vegetation of bog areas, from which 16 additional species were listed. The vegetation cover is complete, and overlies considerable bodies of peat. For all this development the maximum time available is but two centuries. It is remarkable how rapidly a rich and varied vegetation may become established upon newly formed glacial deposits, provided sources for seed and spores are close at hand.

Aside from the foreland, the region adjacent to the bay yielded but nine additional species (two appearing also on the foreland). This is due in part to comparatively thorough previous exploration, coupled with lesser emphasis upon listing and collection on the last expedition.

It seems certain, however, that invasion of recently vacated areas, relatively remote from the ice limit at its recent maximum, is still proceeding very slowly. The bulk of the vegetation is still made up of a few species. Some idea of the rate of progress may be gained from Station 26, a typical pioneer locality in 1916 with an ice-free history of 37 years. Species lists covering approximately the same area were made in 1916 and 1935. In the former year 21 species were found, in the latter 50, including 17 of those listed in 1916. Among the list of 1935 are six previously unreported from the Glacier Bay region. The remainder had already been found in other pioneer localities.

COLLECTIONS BY DAVID BRINK, 1936

In 1936 a glaciological expedition forming a part of Mr. Bradford Washburn's exploratory program spent several weeks in the vicinity of Crillon Lake on the west flank of the Fairweather Range. Mr. Russell Dow was the leader, and Mr. David Brink, then a student at the University of Minnesota, was a member of the party. Mr. Brink, although not a botanist, brought back an excellent and representative collection of the local flora. The list is worth publishing because the region in which the collection was made, being very difficult of access, had been heretofore unexplored botanically. It is a narrow strip of coastal land lying between the ocean and the lofty, ice-covered Fairweather Range, which makes an effective barrier on the east. Glaciers descend at one point to the beach and to tidewater in Lituya Bay. At several other pionts they almost reach the shore. The glacial history is in marked contrast to that of Glacier Bay on the other side of the range. Advance is the order of the day and there has been no general retreat for several decades at least. Within recent months the region between the Fairweather Range and the ocean has been added to the Glacier Bay National Monument.

A total of 87 collections yielded 65 species. Detailed comment on habitats is not possible; it may be noted, however, that the principal communities represented are alpine meadows, pioneer aggregations near glaciers, and climax spruce-hemlock forest. The list follows:

Lycopodium sitchense Rupr.
Chamaecyparis nootkatensis (Lamb.) Spach.
Picea sitchensis Carr.
Tsuga heterophylla (Raf.) Sargent
Tsuga mertensiana Carr.
Calpodium wrightii Scribner and Merrill (*Poa wrightii* Hitchc.)
Deschampsia atropurpurea (Wahl.) Scheele
Festuca ovina brachyphylla (Schult.) Piper

Phleum alpinum L.
Luzula piperi (Cov.) Jones
Streptopus amplexifolius americanus Schultes
Populus trichocarpa T. & G.
Salix sitchensis Sanson
Alnus rubra Bong.
Alnus sinuata (Regel) Rydb.
Oxyria digyna (L.) Hill
Stellaria longipes Goldie
Anemone narcissiflora L.
Caltha leptosepala DC.
Ranunculus bongardi Greene
Ranunculus cooleyae Coult. & Rose
Arabis lyrata glabra (DC.) Hopkins
Arabis pycnocarpa glabrata (T. & G.) Hopkins (*A. hirsuta*, authors)
Heuchera glabra Willd.
Leptarrhena pyrolifolia (Don) R. Br.
Ribes bracteosum Dougl.
Saxifraga bongardi Presl
Saxifraga nelsoniana Don
Tellima grandiflora (Pursh) Douglas
Aruncus sylvester Kostel. (*A. vulgaris* Raf.)
Geum calthifolium Menz.
Geum macrophyllum Willd.
Lutkea pectinata (Pursh) Kuntze
Rubus arcticus L.
Rubus spectabilis Pursh
Sorbus sitchensis Roem.
Lupinus nootkatensis Don
Viola glabella Nutt.
Viola langsdorfii Fischer
Epilobium hornemanni Reichenb.
Epilobium latifolium L.
Fatsia horrida (Sm.) B. & H.
Cornus canadensis L.
Cassiope mertensiana (Bong.) G. Don
Cassiope stelleriana (Pall.) DC. (*Harrimanella stelleriana* (Pall.) Coville
Cladothamnus pyrolaeflorus Bong.
Loiseleuria procumbens Desv.
Menziesia ferruginea Smith
Phyllodoce glanduliflora (Hook.) Coville
Vaccinium caespitosum Michx.
Vaccinium ovalifolium Smith
Vaccinum uliginosum L.
Dodecatheon pauciflorum (Durand) Greene
Primula cuneifolia Ledeb.
Gentiana calycosa Griseb.
Nephrophyllidium crista-galli (Menzies) Gilg.
Castilleja pallida subsp. *elegans* (Ostenfeld) Pennell
Mimulus langsdorfii Donn
Veronica alpina L.
Sambucus melanocarpa Gray
Valeriana sitchensis Bong.
Campanula lasiocarpa Cham. and Schlecht
Achillea borealis Bong.
Anaphalis margaritacea occidentalis Greene
Arnica latifolia Bong.
Erigeron peregrinus (Pursh) Greene
Hieracium gracile Hook.

Determinations of the Glacier Bay materials have been checked by Dr. Paul C. Standley, except for the grasses, which were referred to Mrs. Agnes Chase. Mr. Brink's collections were checked by Dr. Julian A. Steyermark.

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Some Reactions of the Vegetation in the Towns and Cities of Nebraska to the Great Drought

Raymond J. Pool

That unusually severe drought prevailed for months at a time in the northern prairie and plains area of the United States from 1933 to 1938 has become widely known. The dependence of the people of this area upon the products of the land has become emphatically emphasized even to those most widely separated from farm problems in their social and routine contacts of daily life. The paralyzing effects of the drought greatly intensified the suffering of the people in this area, suffering that had been associated with the nation-wide depression which was well developed before crop failure and dust storms swept over the prairies. Black blizzards and cosmic winds that spread a pall of dust from the Trans-Missouri prairies to the Atlantic seaboard carried an impressive message of some of the more obvious natural conditions of the time.

The devastating influence of the drought throughout a vast territory has become best known because of its relation to the ruination of crops and the shortage of feed for livestock. The consequent failure of hundreds of small-town banks and thousands of farmers, and the intensification of unfavorable industrial and economic conditions throughout the area are other natural reactions that have attracted the attention of the nation. Much has been written concerning the effects of recurring drought upon the native and introduced plant life and crops of the region. Many biologists, conservationists, economists, and farmers have wondered if man has not seriously erred in attempting to introduce too widely the types of land utilization which have been proved sensible under more favorable and dependable climatic setups. Widespread interest in man's relationship to natural balances has been created by the disaster. At any rate we are now thoroughly aroused over the situation and tremendous efforts are being pushed by the federal government and various states to trace the causes and to find a way out of the misery. We have here an extremely complex but intriguing problem of first magnitude in the general field of ecology.

As one dry year followed another additional evidences of the destructive effects of increasing water deficiency became prominent. Crop failure was intensified, pastures became thin and poor, quick-growing, shallow-rooted weeds became prominent everywhere. Subsoil moisture was depleted to such a degree that deep-rooted native plants, and crops began to

die or failed to mature. Extremely high temperature and sweeping winds continued to rob the soil and every growing thing of their water supply to an alarming degree. Deep-rooted shrubs and trees began to show the unmistakable symptoms of severe water depletion. Insects and other organic pests took additional toll of every living plant during these troublesome years.

The plant life of our cities and towns mirrors many aspects of the severe damage that the long years of drought have produced in the fields and in the native prairies and woodlands. The most conspicuous effects are noted by the casual observer in the damage which was done to the trees of our urban communities. Many of the larger trees were either killed outright or were badly crippled during the first two or three years of the drought. As dry conditions continued and the subsoil became drier the effect upon the trees of streets, lawns, and parks became more and more prominent. Many of our people were puzzled about the matter at first, and they often sought to explain the loss of trees by reference to borers or other obvious pests. It was difficult to believe that there could not be sufficient water in the deeper soil to supply the demands of our trees, especially for trees along the streams. The trees in town were watered, and still many of them perished. The natural water balance was so severely disturbed that practically all of the older trees began to show the creeping influence of a lowering water table. Fifty per cent or more of the trees of many of our towns died. Since the largest and oldest trees were most severely involved the condition became unusually noticeable. Unsightly conditions appeared everywhere because of the dead trees. Severely pruned and pollarded cripples stood along every street. Large old trees felt the ravaging effects of severe conditions more acutely than did the smaller and younger individuals. The most of the dead trees were removed after a year or two, thus opening the lawns and parkways to the more direct influence of sun and wind. Cities installed saw mills in which logs from the stricken trees were cut into hundreds of cords of firewood and even into thousands of feet of lumber.

Observations on the effects of the protracted drought of the 1930's upon our trees have corroborated to a striking degree various conclusions which have grown from studies of such phenomena dating back to the time when the pioneers of the prairie began to plant trees here. One of these conclusions that the latest drought emphasizes is that the prairies are relatively treeless because of the natural conditions that prevail here now. The prairie represents an ecological complex that is likely to be

inimical to the life of trees and even suddenly death-dealing in its severity upon trees. The prairie is characterized positively by a broad, sweeping landscape which is dominated by grasses and their low-growing, drought-resisting associates. The prairie is also characterized negatively by the relative absence of trees.

The drought has also emphasized the reliability of our earlier judgment concerning the relative adaptability of various kinds of trees for artificial culture in the cities and towns of the prairie region. But we know now, better than ever, what kinds of trees are most likely to succeed and to survive (even when old and large) and which ones are most likely to be damaged and killed by continued dry weather. The trees have been exposed to a test during these years that has been so severe and protracted as to reveal the stability of the most drought-resistant types.

Botanists and tree specialists know that the relative position of different species in a scale of drought resistance and drought endurance is markedly influenced by the age and size of the individual tree. A citizen may feel that a certain tree, say the hackberry, is unusually good for planting under our conditions because of the fact that his hackberry lived through the drought, and that the basswood was a poor tree to use, because the latter tree on his lawn had died. But the hackberry in this instance may have been a small, young tree and the basswood a much larger, older tree. Or again, the former tree may have been growing in a spot that enjoyed much better water relations than the latter. Such common observations as the above suggest that our scale of drought resistance must be made only after a study of the behavior of the different trees of various ages and under a wide variety of environmental conditions.

Our wide study of the behavior of planted trees in the Nebraska region for forty years, including the extremely severe recent drought period, indicates that the hackberry (*Celtis occidentalis*) should be placed at the top of the list for dependability to endure and to live through long periods of severe drought. Other trees may be, and indeed are preferred, by many of our citizens, for various sensible reasons, but we are not concerned with those reasons at this time. We must understand that the "miracle," if indeed there is one at all, in the severe relationships of planted trees to the prairie complex, is not in the fact that thousands and thousands of trees have been killed by the dry weather, but that any of them have survived! The hackberry stands out as our most successful tree in this matter as we examine all features of the problems

involved. And yet, even a good many hackberry trees (especially large, old ones) perished during the years of the great drought.

The persistence of the honey locust (*Gleditsia triacanthos*) and the green ash (*Fraxinus pennsylvanica* var. *lanceolata*) has also been notable in the face of the extreme conditions of the drought. I place the former in the number two position in my list, since it unquestionably endures great extremes of desiccation (and accompanying troubles) at various age and size classes, and under the great variety of conditions in which we plant our trees. Insect troubles (particularly borers) have been prominent in the green ash.

Silver maple (*Acer saccharinum*) and the sycamore (*Platanus occidentalis*, very little *P. orientalis* and *P. acerifolia*) have also withstood the rigors of the time remarkably well. These have lived through the stress even in the form of large trees when they have occupied the most favorable sites. But the silver maple, being one of the earliest and most widely planted species, presents a miserable picture, in general, because of the damage and loss to a great many of the fine old and large trees.

The white elm (*Ulmus americana*) has also been widely planted and beautifully successful over a wide territory, but the older, finer specimens of this species have suffered severely. Many of the drought stricken elms have become extremely bristly on account of the formation of dense fringes of "sap sprouts" along the trunk and large branches. Such trees have been severely cut back and bluntly topped, a treatment that still further adds to the ugly aftermath of the drought. The red elm (*U. fulva*) has not been planted in such numbers as the white elm, but the larger trees of this species have been seriously damaged and many of them have died.

Besides the above trees, all of which are native to eastern Nebraska, many additional species have been planted in our cities and towns, along with numerous other kinds that do not occur here naturally. The native cottonwood (*Populus Sargentii*), glorious tree of the pioneers, was planted in large numbers (as single trees, in rows, and in groups) during the earlier years in the settlement of the state. Most of them had matured and practically reached the end of their life span in the cities, and had been replaced by other species before the inception of the great drought. A few magnificent old specimens of the cottonwood remained here and there and they were among the first of our trees to succumb with the onset of the drought. The loss of these monarchs of the prairie (so rich in pioneer lore) was really the prologue of the more terrible tragedy that

was to overtake other species in the years to follow. The great decorticated, white trunks and large diverging branches of those old cottonwoods were (and still are in places) ghostly evidences of a peculiarly impressive reaction to the deficiency of available soil moisture.

Many other species and varieties of broad-leaved, deciduous trees have been tried out through the years as planted intruders of the treeless grasslands. Such trees as boxelder (*Acer Negundo*), sugar maple (*Acer Saccharum*), Norway maple (*Acer platanoides*), black walnut (*Juglans nigra*), American and European linden (*Tilia glabra, T. europaea*), white poplar (*Populus alba*, inc. var. *bolleana*), Carolina poplar (*P.* sp.), white oak (*Quercus alba*), bur oak (*Q. macrocarpa*), northern red oak (*Q. borealis*), pin oak (*Q. palustris*), white ash (*Fraxinus americana*), and paper birch (*Betula papyrifera*) have been planted with variable success under widely differing conditions. Most of these have suffered severely, but it must be stated that the bur oak and even the pin oak (a lowland tree) have shown unusually fine or encouraging fortitude under the circumstances. Much of the success of the pin oak is explained by the fact that these trees were so highly regarded by the owners that they were given sufficient water from the hose to tide them over the troublesome months when other trees were being killed by the thousands. The bur oak is by nature one of the most drought-resistant of the oaks, a fact that has been reflected in its persistence through the years of ecological stress. The rapid-growing Chinese elm (*U. parvifolia*) has been widely planted in recent years as a street tree in the prairie region, and its behavior during the drought has been encouraging. We should, however, reserve our judgment with reference to the place of this tree under the conditions of periodic drought because of the fact that few of the trees had reached an age and size that would constitute a conclusive test.

We should also summarize our observations as to the behavior of planted needle-leaved evergreens in the face of the prolonged drought. The really outstanding feature of this situation is seen in the remarkably slight destruction that has befallen such trees as the native red cedar (*Juniperus virginiana*) and many of its cultivated varieties. This species has been prominent for years in the form of fine individuals in lawns and parks, and in rows as windbreaks on the farms. These trees, in general, have been damaged slightly if at all. The Austrian pine (*Pinus nigra*) and the Scots pine (*P. sylvestris*) have also survived to an encouraging degree. The Michigan white pine (*P. strobus*), sparingly planted, suf-

fered severely in most places, as did such fine trees as white spruce (*Picea glabra*), blue spruce (*P. pungens*), Norway spruce (*P. excelsa*), balsam fir (*Abies balsamea*), and white fir (*A. concolor*). The Douglas fir (*Pseudotsuga taxifolia*) has been sparingly planted in cities and towns on the prairies and it has withstood the drought to a surprising degree, but there again, the individuals of this species were commonly too young and small during the dry years to yield dependable information as to what they would do when they had become much larger. It is true that many home owners watered their evergreens sufficiently to prevent much of the damage to their trees that would surely have occurred if nature's supply of precipitation had not been supplemented.

Planted ornamental shrubs also suffered badly. The shrubs that have been most widely and successfully used as lawn plants and hedges in eastern Nebraska are the bridal wreath (*Spirea Vanhouteii*), the Amur privit (*Ligustrum amurense*), and the Japanese barberry (*Berberis Thunbergii*). Older hedges and larger isolated groups of all these were severely damaged by the drought, many of them being completely killed, or so badly disfigured as to necessitate replanting. The privet has shown a much greater degree of drought resistance than the others under a wide variety of conditions. Other broad-leaved deciduous shrubs such as golden-bells (*Forsythia suspensa*), tatarian honeysuckle (*Lonicera tatarica*), mulberry (*Morus* sp.), and the pea tree (*Caragana* sp.) were commonly killed in toto or they died back and the tops thinned to a degree that made them unsightly.

Evergreen shrubs (*Thuja* and *Juniperus*) grown as hedges have withstood the rigors of the drought to a surprisingly high degree. Such survivals have been due in certain instances to a supplementary water supply in connection with lawn watering. Broad-leaved evergreen shrubs are rarely planted in Nebraska.

Conspicuous and astounding changes also spread over the lawns, parkways, and golf courses in city and town as a result of long periods when there was little or no available moisture in the soil to depths of three to six feet, and when parching winds swept across the land. Long years of experimentation had perfected various lawn-grass mixtures that could be depended upon to make a good lawn (with more than ordinary care) in Nebraska. Bluegrass, especially Kentucky bluegrass (*Poa pratensis*) was the most significant ingredient of this lawn-grass mixture. When the soil was carefully prepared and the seeding (or sodding) well done, about all that the home owner had to do to insure the development

and maintenance of a good lawn was to apply water in sufficient quantity, keep the lawn properly fertilized and mowed, and then wage a continuous and vigorous battle against the threat of weeds. Among the more troublesome weeds in this picture were the dandelion (*Taraxacum officinale, T. erythrospermum*), water grass (*Digitaria sanguinalis*), and a host of lesser species that might become pestiferous if the necessity for eternal vigilance was overlooked. In late years the very worst weed of all, namely the bindweed (*Convolvulus arvensis*) has become prominent as a severe lawn pest.

As the drought continued year after year numerous property owners and lessees became wearied by the battle of trying to keep a good lawn against such tremendous odds. In a region where the maintenance of a lawn even under the best of natural conditions is a difficult task it is not surprising to find that many city dwellers gave up the fight and left their lawns to whatever fate nature might dictate. The common initial reaction noted in the lawns was the prompt thinning and killing of the bluegrass. When the grass was dead and brown any deep-rooted perennial and drought-resistant weed, such as the dandelion, became more and more evident. Such weeds profited at once from the complete subjugation of the lawn grasses and the removal of the competition involved. The ground often became densely covered by a choking growth of such plants. The complete invasion of the dandelion was but one example of similar situations in which the principal rôle was taken by other persistent species such as bindweed (*Convolvulus arvensis*), the puncture vine (*Tribulus terrestris*), henbit (*Lamium amplexicaule*), and others. Numerous main lawns and parkways (between sidewalk and curb) were seen in which one or the other of these ruinous species formed a complete cover over thousands of square feet.

When the bluegrass was killed in lawns where there were few or no deep-rooted perennial weeds, the bare areas were often quickly captured by such weeds as shepherd's purse (*Capsella Bursa-pastoris*), pepper grass (*Lepidium apetalum*), and penny cress (*Thlaspi arvense*), which produced a growth so dense and rank that all other invaders were repelled. Practically pure stands of these vigorous weeds were common sights in vacant lots and lawns that but a short time previously had been covered by fine bluegrass. Summer cypress (*Kochia scoparia*), lamb's quarters (*Chenopodium album*), Russian thistle (*Salsola Pestifer*), knotweed (*Polygonum aviculare*), false flax (*Camelina sativa*), milk purslane (*Euphorbia maculata*), and henbit (*Lamium amplexicaule*), were additional invaders

of weakened and bare lawns and all these became prominent during the drought. The mare's tail (*Erigeron annuus*) and the many-flowered aster (*Aster multiflorus*) were likewise common invaders and often became impressively dominant. As lawn conditions became increasingly severe many people came to welcome the presence of a dense growth of green weeds on their lawns. Such conditions were certainly to be preferred over the bare, hot, dusty and plantless expanses that one frequently noted.

One of the most interesting aspects of the sweeping succession of changes that were seen in our lawns in their reactions to the drought was the complete invasion and subjugation of many vacant lots and lawns by certain xerophytic grasses. The presence of downy chess (*Bromus tectorum*) in poorly kept or abandoned lots and lawns was a rather common condition long before the inception of the great drought in 1933. This annual weed was sometimes a real nuisance in such places, but its behavior was greatly expanded and intensified by the drought. Other annual grasses, not so often observed in this rôle before the drought, which frequently "took" lawns were certain species which are often called "poverty grasses," such as *Sporobolus neglectus*, *S. vaginiflorus*, prairie three-awn, *Aristida oligantha*, and six-weeks fescue, *Festuca octoflora*. These species invaded thousands of the bare and abandoned lawns, and large areas in parks and golf courses where they practically covered the surface to the exclusion of all other plants.

We have recorded only the more common and conspicuous reactions and changes in the plant life of our lawns and parks that have occurred during the great drought. It is already apparent, as conditions in 1938 indicate, that our people may again hope to have good lawns whenever nature supplies a more nearly normal rainfall during the critical summer months for several years in succession. But most certainly the establishment and upkeep of good lawns will remain a difficult and puzzling problem because of the aftermath of conditions (both physical and biological) spread over this vast prairie region by the great drought.

DEPARTMENT OF BOTANY
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A Flora of Eastern American Aspect in the Miocene of Idaho*

HELEN V. SMITH

(WITH PLATES 10–13)

A preliminary study of a fossil flora from Thorn Creek, Idaho, shows that the aspect of the flora is typically modern and immediately suggests the climax deciduous forest of the eastern United States. There are three important floristic elements and one minor one, namely (1) those species whose nearest living equivalents now grow in eastern America, (2) those now represented by living allies in the flora of the humid Pacific coast region, (3) those whose modern representatives are found in the high mountains of the West, and (4) a smaller number that have modern living equivalents in the Southwest. The eastern American element is so distinctive and interesting that the most characteristic species of it are published here in advance of a comprehensive report on the flora.

Thorn Creek, a mountain stream flowing west from Thorn Creek Mountain empties into Moore Creek, a tributary of the Boise River, at an elevation of about 3500 feet, approximately ten miles south of Idaho City, and about twenty miles northeast of Boise, Idaho. The fossil bearing beds from which the material for this study was obtained are exposed in a road cut on the south side of the valley. The matrix is a very fine grained, light colored volcanic ash in which the specimens are found unequally distributed. The preservation of the impressions is excellent and the finest details of venation can be made out readily with the aid of a lens. About three thousand specimens were examined, of which one-third were retained for laboratory study.

The following is a list of the Thorn Creek species that have as their nearest living equivalents species now occurring in the eastern United States.

Fossil species	*Living species*
Betula idahoensis H. V. Smith	*B. lenta* L.
Carpinus sp.	*C. caroliniana* Walt.
Celastrus sp.	*C. scandens* L. (?)
Fagus washoensis LaMotte	*F. grandifolia* Ehrh.
Fraxinus sp.	*F. quadrangulata* Michx. (?)
Magnolia oregoniana Chaney	*M. virginiana* L.
Populus washoensis R. W. Brown	*P. grandidentata* Michx.

* Papers from the Department of Botany and of the Botanical Gardens of the University of Michigan, No. 692.

Pteris calabazensis Dorf	*P. aquilina* L.
Quercus Eoprinus H. V. Smith	*Q. prinus* L.
Quercus Maccannii Berry	*Q. bicolor* Willd.
Quercus Merriami Knowlt.	*Q. rubra* L.
Rhododendron idahoensis H. V. Smith	*R. maximum* L.
Salix Schimperi Lesq.	*S. cordata* Muhl.
Ulmus paucidentata H. V. Smith	*U. alata* Michx. (?)

Of the species in the above list *Pteris calabazensis* and *Salix Schimperi* have as their living equivalents species which are not confined to the eastern United States. *P. aquilina* is one of the most widely distributed plants known. *Salix cordata* is also found in the Rocky Mountains and Pacific coast states.

In addition to the recorded species, there are a number of maple leaves that are very much like *Acer rubrum* L. They are not included in the list because of their equally close similarity with *A. glabrum* var. *Douglasii* (Hook.) Dippel of the west. *Quercus pseudolyrata* Lesq. is quite abundant and is probably about as close to certain eastern oaks as it is to the California species, *Q. Kelloggii* Newb., which is now usually considered to be its living equivalent.

Three species are represented only by fruits or bracts and will not be named at present because more material is to be collected and leaf impressions of those species may be encountered. *Fraxinus* is represented by several samaras, but the *Celastrus* and *Carpinus* are each represented by a single specimen and its counterpart.

Quercus and *Fagus* are the most important genera in point of abundance. *Quercus Eoprinus*, a typical chestnut oak of Appalachian aspect, is represented by more material than any other species. *Quercus* no longer occurs in southern Idaho, but is found in Oregon west of the Cascade Mountains and in California. Chestnut-leaved oaks no longer grow in the west. *Quercus* is a large genus with several hundred described species which inhabit the temperate regions of the Northern Hemisphere and medium altitudes in the tropics. In the Americas it ranges as far south as the mountains of Colombia; in Asia it extends south to the Indian Archipelago. *Fagus* is second only to *Quercus* in number of specimens. All of the material collected to date at Thorn Creek can be assigned to a single species. Of the eight recognized living species only one is now found in America. This and the fossil form are very much alike as to leaves, burs, and nuts. The living species is widely distributed in the

eastern United States in rich uplands, and on the bottomlands of streams and along the borders of swamps. One species is found over a great part of Europe. The others are found in the temperate region of eastern Asia and in the Caucasus. If the Appalachian flora is, as botanists believe, a relatively unmodified vestige of vegetation which was much more widely distributed during the Miocene, it is quite in accordance with expectation to find a single beech of eastern aspect in the western Miocene.

SYSTEMATIC DESCRIPTIONS

PTERIS CALABAZENSIS Dorf
Plate 12, fig. 2

Pteris calabazensis Dorf, Carnegie Inst. Wash. Pub. 412: 67, pl. 5, figs. 1, 2, 1930.

A single small fragment including about eight pinnules is the only fern so far discovered at Thorn Creek. There are no sori present so a convincing generic determination cannot be made. However, the fossil seems to be very similar to *Pteris* (*Pteridium*) *aquilina* L. It can be duplicated in size, shape and venation on certain fronds of this variable living species. Dorf's specimens from the Pliocene of California are likewise similar and are also very much like the Thorn Creek specimen. The fern fragment from Salmon, Idaho, figured by Brown (2) is probably also this species. It is also possible that *Dryopteris idahonensis* Knowlt. described from Montour, Idaho, is the same.

The common brake is of world-wide distribution. It is common in Canada and in the northern half of the United States where it grows in woods and open sandy places. In the humid Northwest it grows luxuriantly and attains considerable size. In drier habitats it is smaller. It is often associated with aspens and is found in open pine forests in the lower mountains of Idaho.

POPULUS WASHOENSIS R. W. Brown
Plate 10, fig. 1

Populus washoensis R. W. Brown, Jour. Wash. Acad. Sci. 27: 12, 516, 1937.

Populus Lindgreni Knowlt. LaMotte, Carnegie Inst. Wash. Pub.: 455; 115, pl. 4, fig. 1, 1936.

P. washoensis was first found in the Upper Cedarville formation of Nevada and illustrated as *P. Lindgreni* Knowlt. Since there are

several good specimens in the Thorn Creek collection and no description of the species has been previously published, one is included here.

Leaves firm, very thin, orbicular, sometimes broader than long; average length 5 cm., average width 5.3 cm.; margin irregularly coarsely crenate-dentate, teeth forward pointing, not entered by a prominent vein; apex abruptly short acuminate; base broad, often slightly cuneate; midrib fairly firm below, tapering, weak above, often curved at the point of origin of the secondaries; secondaries 4 or 5 pairs, the lowest giving off 2–4 abaxial tertiaries; secondaries somewhat irregular, often forking, ending in fine nervilles before reaching the margin; tertiaries fine, forming very irregular to almost percurrent arches between the secondaries; finer venation distinct, forming a coarse irregular or often quadrangular reticulum.

This species is characterized by the very thin texture of the blade, the coarse irregular teeth and distinct ultimate venation. It is very similar to *P. grandidentata* Michx. (Plate 10, fig. 3) which occurs from New Brunswick southward as far as the Great Smoky Mountains of Tennessee and North Carolina and as far west as eastern Minnesota, Iowa and Illinois. It usually grows on sandy slopes and stream banks and may be associated with conifers or such broad-leaved trees as maples, oaks, and service berries.

Salix Schimperi Lesq.

Salix Schimperi Lesquereux, U. S. Nat. Mus. Proc. 11: 21, pl. 8, fig. 5, 1888.

Juglans hesperia Knowlton, U. S. Geol. Surv. Eighteenth Ann. Rept. pt. 3: 723, pl. 9, fig. 8, 1898.

A large number of specimens referable to this species were found at Thorn Creek. It is characterized by the round or cordate base, numerous secondaries and very stout midrib. It was described from a single well preserved specimen from Cherry Creek, Wasco County, Oregon.

S. inquirenda Knowlt. a well known Miocene species first described from the Latah near Spokane, Washington, appears to be very similar,

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Explanation of Plate 10

Fig. 1. *Populus washoensis* R. W. Brown.

Fig. 2. *Betula lenta* L. Specimen in Herb. Univ. Mich., from Linville, N. C., for comparison with *Betula idahoensis*.

Fig. 3. *Populus grandidentata* Michx. Specimen in Herb. Univ. Mich., from St. Clair County, Mich., for comparison with *P. washoensis*.

Fig. 4. *Betula idahoensis* H. V. Smith. Type, Mus. Paleon., Univ. Mich., No. 18696.

so much so that it is difficult to distinguish between them. The principal differences seem to be the usual occurrence of a cordate or rounded base and stout midrib in *S. Schimperi.*

Among living willows these leaves are similar to those of *S. cordata* Muhl., the heart-leaved willow. This is a shrubby species found growing in wet ground from New Brunswick to Virginia, Colorado, California, and British Columbia.

Betula idahoensis n. sp.

Plate 10, fig. 4

Leaf membranaceous, 6.4 cm. long, 3.5 cm. wide, broadly oblong-ovate, narrowed rather abruptly to an acuminate apex and with a broadly cuneate slightly asymmetric base; margin regularly simply serrate except just at the base where it is entire; teeth small, acute, forward pointing, those teeth entered directly by the secondaries the strongest, the 1–3 teeth between the secondaries slightly less prominent but also sharply pointed and each entered by a small, rather weak, abaxial vein; midrib not strong; secondaries about 14 pairs, alternate or occasionally almost subopposite, the lowest pair very weak, arising at the top of the petiole and extending just within the margin for a short distance; the next two pairs arising at a very acute angle and immediately curving outward, those in the midportion of the blade arising at angles of 35–40°, subparallle, straight or curving slightly, terminating in the marginal teeth, sometimes with 1–3 abaxial branches terminating in the teeth; tertiary venation obscure, consisting of very fine irregular percurrent veins; no ultimate venation visible; petiole stout, 6 mm long.

Bract of catkin three lobed, lobes of approximately equal size; lateral lobes divergent, length 6 mm., width 9 mm.

Nut small, obovate, 1 mm. wide, 2 mm. long, terminated by two minute divergent stigmas, surrounded by a membranous wing except at the stigma end, wing widest just below the origin of the stigmas, overall width at widest point 4 mm. Leaf, Mus. Paleon., Univ. Mich., type, no. 18696.

This beautifully preserved leaf is the only one of its kind in the collection. It undoubtedly belongs to the Betulaceae and a study of all available material of that family indicated its affinities with *Alnus* or *Betula.* Among species of *Alnus* it bears some resemblance to leaves of *Alnus sinuata* Ryd., but differs from the latter in the lack of short

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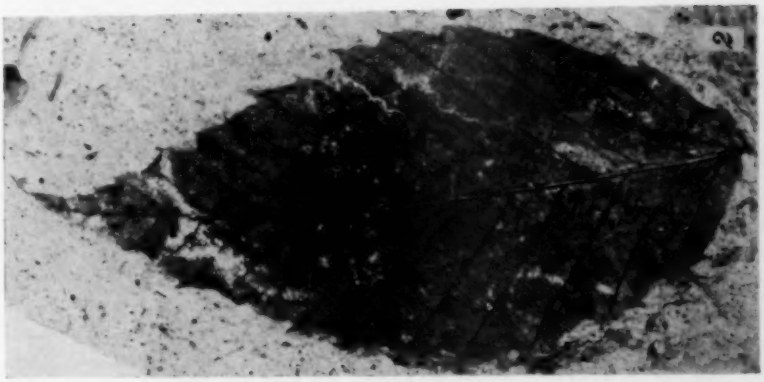
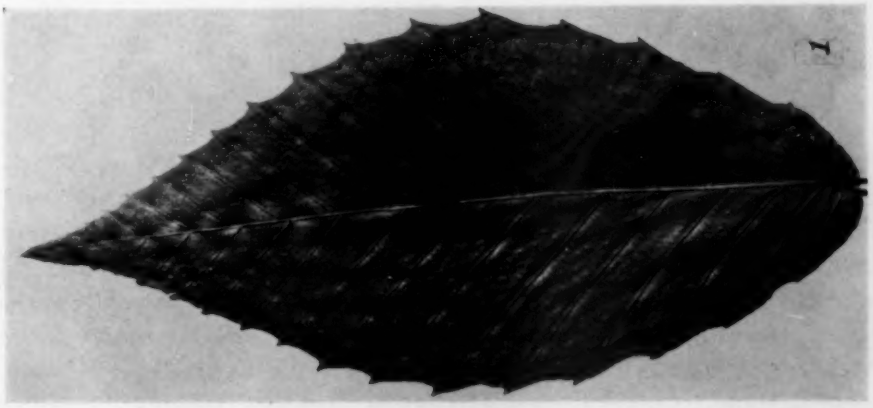
Explanation of Plate 11

Fig. 1. *Fagus grandifolia* Ehrh. Specimen in Herb. Univ. Mich., from Warren Woods, Berrien County, Mich., for comparison with *F. washoensis.*

Figs. 2, 3, 4. *Fagus washoensis.* Fig. 4, nut, ×1½.





SMITH: MIOCENE OF IDAHO

lateral lobes terminating each secondary vein. *Alnus*, therefore, seems to be eliminated as a possibility. *Carpinus* and *Ostrya* are usually conspicuously unequally or doubly serrate and thus unlike the fossil. *Betula lenta* L. (Plate 10, fig. 2) the black or cherry birch of northeastern United States and the Alleghany region has leaves, bracts and seeds which very closely resemble the fossils. In fact certain leaves of the living species are almost exact duplicates of the fossil leaf.

Carpinus sp.

A single bract and its counterpart are the only specimens referable to this genus. In general shape and venation as well as in the strong marginal teeth they are similar to the involucres of *C. caroliniana* Walt. The rather narrow and quite elongated middle lobe is more suggestive of *C. Betulus* L. It is unfortunate and rather surprising that there are no leaves of *Carpinus* in the material obtained from Thorn Creek thus far.

C. caroliniana, the blue beech or hornbeam, is common in the eastern and southern United States. In the mountains of southern Mexico and Central America it is represented by *C. caroliniana* var. *tropicalis*. It reaches its maximum growth on the western slopes of the southern Alleghany Mountains and in southern Arkansas and eastern Texas.

Fagus washoensis LaMotte
Plate 11, figs. 2, 3, 4; Plate 13, figs. 5, 7, 9

Fagus washoensis LaMotte, Carnegie Inst. Wash. Pub. 455: 119, pl. 8, figs. 2, 3, 5, 1936.

Leaves of this species constitute an important element of the Thorn Creek flora. A single bur and a well preserved impression of a nut were also found. *Fagus* is not found in western North America at the present time but the single American species is abundant in the deciduous climax forest of eastern North America where it ranges as far west as Minnesota. It grows best in a deep, rich, well-drained loam, but is also found on a great variety of soils and reaches its best development on the bottom lands of streams in regions where the rainfall is 35–40 inches annually. The existing species of *Fagus* are confined to the North Temperate zone.

Of the two well described and figured species of *Fagus* from the Tertiary of the West the specimens at hand are more like those referred to *F. washoensis* although the distinction between that species and *F. paci-*

fica Chaney from Crooked River, Oregon, is not entirely clear. The Thorn Creek specimens closely resemble those figured by Berry (1) as *F. pacifica* (pl. 19, 20), and later referred to *F. washoensis* by LaMotte. It is because of LaMotte's disposition of Berry's specimens rather than my ability to distinguish two species that this identification of the Thorn Creek material is made. *F. washoensis* has also been reported from Tipton and Austin, Oregon, from the Upper Cedarville formation at 49 Camp, Nevada, and Pit River, California. The larger specimens from Thorn Creek, some of which are indistinguishable from those figured by Berry and referred to above, are very well preserved and show the nature of the margin and venation extremely well. The description of *F. washoensis* indicates that there are usually 15 or more pairs of secondaries although that number is not visible in the photographs of the specimens from Upper Cedarville formation nor are that many common in the Thorn Creek specimens. The teeth in most of the specimens are well marked and the margin should be considered to be distantly and coarsely serrate. The resemblance to *F. grandifolia* Ehrh. (Plate 11, fig. 1) is marked. The margin with strong teeth is unlike that of the figured specimens of *F. longipetiolata* Seeman with which LaMotte compared his specimens. This latter species has the margin undulate or curved in at the end of the secondaries. It is questionable where the differences between *F. pacifica* and *F. washoensis* are significant enough to distinguish two species.

Quercus Eoprinus n. sp.

Plate 12, figs. 3, 4

Leaves membranaceous but firm, 4–10 cm. long, 2.5–5.5 cm. wide, obovate or occasionally broadly elliptic; widest at the middle and narrowed abruptly to the wedge-shaped base which is usually slightly asymmetrical; apex acute; margin coarsely crenate-dentate; teeth triangular, somewhat rounded or acute and usually pointing forward, the upper teeth the smallest and most crowded, those about the middle of the blade the largest; sinuses between the teeth shallow, broad and rounded; midrib quite stout below, becoming very fine and often flexuous above; secondaries usually 11 to 14 pairs, subparallel, close together in the upper third of blade, arising from the midrib at angles of 25–50°, straight, tending to be opposite near the base and apex and alternate between, not forking, ending in the teeth or the lowest pair or two ending in the undulations of the margin; tertiaries very fine, close-set, percurrent, those near the margin not perpendicular to the midrib; ultimate venation a very fine reticulum. Type, Mus. Paleon., Univ. of Mich., no. 18697.

This fine species is obviously similar to the chestnut oaks of the Atlantic region of the United States. These oaks are characterized in part by their lanceolate or usually obovate coarsely sinuate-toothed leaves. Among the living species studied a close resemblance was found between the fossil leaves and *Q. Muehlenbergii* Engelm., *Q. prinoides* Willd. and *Q. Prinus* Auct. (non L.) = *Q. montana* Willd. fide Sargent. All three species differ from the Thorn Creek material in being larger-leaved, and *Q. Muehlenbergii* tends to have the leaves narrowly elliptic-ovate with rather pointed teeth. *Q. prinoides*, the chinqua pin oak, has fewer, coarser teeth which are spaced farther apart than those of the fossil; its leaves are often elliptic instead of obovate. The greatest similarity is found with *Q. Prinus* Auct. (Plate 12, fig. 1). This common chestnut oak grows on hillsides and high rocky banks of streams. It is found from New England along the coast to Delaware, and southward along the Appalachian Mountains to Georgia. It extends westward to western New York state, southern Ohio and southern Indiana to central Tennessee and Kentucky. It reaches its largest size and is most abundant along the banks of the lower Hudson River and on the Appalachian Mountains. In the Great Smoky Mountains it often forms a large part of the forest and may reach elevations of 4000 to 5000 feet.

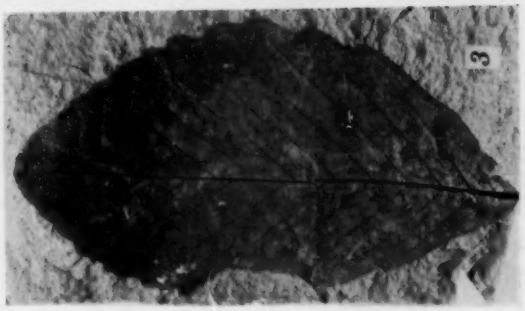
Quercus Maccanni Berry, described from the Grand Coulee and found also at Thorn Creek, is somewhat similar. Its leaves are generally coarser, with fewer secondaries, a stronger midrib, a wider angle formed by the secondaries and the midrib, and coarser tertiary venation. *Quercus spokanensis* var. *gracilis* Berry from southeast of Montour, Gem County, Idaho, is strikingly similar and may be the same species as the Thorn Creek specimens. I do not believe that this nominal variety is similar enough to *Q. spokanensis* to be included with the latter. There is also some doubt as to whether *Q. spokanensis* is even a *Quercus*. It was described from a fragmentary specimen that Brown (3) believes should be referred to *Castanea*. The smaller leaves somewhat resemble the Miocene *Q. Applegatei* Knowlt. found near Ashland, Oregon.

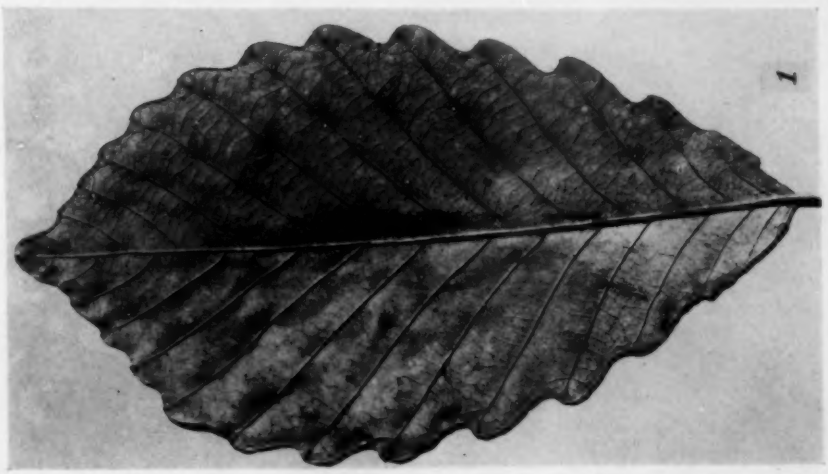
Explanation of Plate 12

Fig. 1. *Quercus Prinus* L. Specimen in Herb. Univ. Mich., from Sheffield, Ala., for comparison with *Q. Eoprinus*.

Fig. 2. *Pteris calabazensis* Dorf. ×3.

Figs. 3, 4. *Quercus Eoprinus* H. V. Smith. Fig. 4, type, Mus. Paleon., Univ. Mich., No. 18697.





SMITH: MIOCENE OF IDAHO

Quercus Merriami Knowlt.
Plate 13, fig. 8

Quercus Merriami Knowlton, see Brown U. S. Geol. Surv. Prof. Paper 186: 172, 1936, for synonymy.

Since *Quercus ursina* Knowlt. and *Q. Merriami* Knowlt. are considered (as suggested by Brown) to be synonyms of the same species, a new description including both of these forms is given.

Leaves subcoriaceous, firm; ovate elliptic or slightly obovate to broadly lanceolate in outline; lobed, the lobes tapering rather abruptly to the pointed apex, sometimes with one or two sharp teeth on each of the principal lobes in the larger leaves; lobes 2 to 4 pairs, at times unequal in number on the two sides of the blade, alternate or subopposite, deltoid; sinuses moderately wide, decidedly oblique; midrib moderately strong, sinuous, tapering; principal secondaries alternate, the same number as the lobes and terminating in their apices, at times forking to give off branches to the lateral teeth, arising obliquely at an angle of 25 to 45°; intermediate secondaries few, weak, apparently craspedodrome; tertiaries few, fine, somewhat irregular; ultimate venation obscure; apex of leaf acute, at times sparsely dentate, base cuneate to rounded-truncate; petiole rather long (over 1.5 cm.) and slender; length of leaf 2.5–15 cm. (estimated) and width 1.4–6 cm. between tips of lobes.

Q. Merriami as here interpreted is characterized by being deeply obliquely lobed, the lobes tapering, triangular, and frequently with a single tooth.

A study of living species shows some similarity (especially of the smaller leaves) with *Q. ilicifolia* Wang., the bear oak or scrub oak of dry sandy barrens and rocky hillsides on the eastern slope of the Appalachian Mountains and along the New England coast. Still closer is *Q. rubra* L. (Auct., non Sargent) among the many leaf types of which most specimens of *Q. Merriami* can be duplicated. The red oak is very common and is found from Nova Scotia southward in the Appalachians and west to Minnesota, eastern Kansas and Oklahoma. In the Appa-

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Explanation of Plate 13

Fig. 1. *Ulmus alata* Michx. Specimen in Herb. Univ. Mich., from Swain County, N. C., for comparison with *Ulmus paucidentata*.

Figs. 2, 3, 4. *Ulmus paucidentata* H. V. Smith. Fig. 2, type, Mus. Paleon., Univ. Mich., No. 20016. Fig. 4, a portion of leaf in fig. 2, ×3.

Figs. 5, 7, 9. *Fagus washoensis*. Fig. 5, bur, ×1½. Fig. 9, a bud scale, ×1½.

Figs. 6, 10. *Rhododendron idahoensis* H. V. Smith. Fig. 6, a portion of leaf shown in fig. 10, ×3, to show venation. Fig. 10, type, Mus. Paleon., Univ. Mich., No. 20018.

Fig. 8. *Quercus Merriami* Knowlt.

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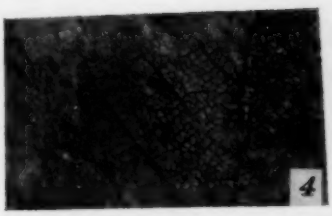
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lachians of North Carolina it may reach elevations of 4000 feet. It is one of the largest and most widely distributed trees of the northern states.

Q. Merriami was described from the Mascall flora at Van Horn's Ranch in the John Day Basin of Oregon, and has since been reported from the Latah at Spokane and the Grand Coulee, Washington.

Quercus Maccanni Berry

Quercus Maccanni Berry, U. S. Geol. Surv. Prof. Paper 170: 36, pl. 11, figs. 5, 6, 1931.

These leaves representing a species of chestnut-leaved oak were described from the Latah flora of the Grand Coulee, Washington, and apparently have not been reported from any other locality. The coarse oblique rounded teeth are often slightly irregular in spacing and size and begin a short distance above the base which is cuneately narrowed to the rounded petiole insertion. The sinuses are rounded and oblique, the midrib strong, the secondaries thick and prominent. The percurrent tertiaries are usually 2–3 mm. apart and almost perpendicular to the secondaries.

The leaves of this species possess characters in common with those of the swamp white oak, *Q. bicolor* Willd. This oak inhabits low borders of streams and swamps from southern Maine west through southern Ontario and central Michigan south to the Ohio River and southeastern Nebraska. It extends south along the Alleghanies to northern Georgia and east of the mountains as far south as the District of Columbia. It grows with maples, sour gum, other oaks, and ashes. It is nowhere abundant but is most common and attains its largest size in western New York and northern Ohio.

Ulmus paucidentata n. sp.

Plate 13, figs. 2, 3, 4

Leaves membranaceous, straight or curved, narrowly ovate-elliptic 2.5–5 cm. long, 1–1.8 cm. wide, gradually narrowing to an acute, somewhat attenuate apex; base narrowly cuneate on one side, rounded on the other, or the small leaves are apparently rounded on both sides; margin obscurely doubly dentate, the teeth entered by the veins being quite large, obtusish, subascending, with one or two minute teeth on the basal side, or entire; midrib moderately stout, straight or curved; secondaries straight, subparallel, terminating in the coarse teeth, 10–13 pairs on the rounded side, 9–11 pairs on the cuneate, arising on the cuneate side at angles of 37–43°, and on the other at angles of 45–50°;

no distinct tertiaries, ultimate venation rather finely reticulate; petiole curved, at least 1 cm. long. Type, Mus. Paleon., Univ. Mich., no. 20016.

The small size, asymmetric base and obtuse teeth characterize this species. Most species of *Ulmus* have larger leaves but the following were found to have leaves that are sometimes the same size of those of the fossil species: *U. parvifolia* Jacq., *U. crassifolia* Nutt., *U. pumila* L., and *U. alata* Michx. None was found to be very similar to the fossil species, but all had certain characteristics in common with it.

U. parvifolia, the Chinese elm of China, Korea, and Japan, differs in that the leaves are usually widest above the middle, less cuneate on the narrow side, with the teeth more pointed and spreading rather than ascending, with no small secondary teeth and a less attenuate apex. *U. crassifolia*, the common cedar elm of Texas, is subcoriaceous, round-elliptic or nearly oblong and with veins less regularly spaced. The secondaries are forked more frequently and the margin may or may not be doubly dentate. The teeth are smaller and less prominent. *U. alata* is quite similar to the Thorn Creek species in size and appearance of the teeth (Plate 13, fig. 1). It differs in its more conspicuous and more numerous accessory teeth and in being more symmetrical at the base. *U. pumila* is also somewhat similar. Its leaves are small, not very asymmetric, but rather narrowly ovate. They are usually but not always doubly serrate and occasionally show forking of the secondaries. This is the dwarf Asiatic elm native to northern China, eastern Siberia and Turkestan. Among these elms, *U. alata* seems to be the most similar to the fossil species. The wahoo or winged elm is native from Virginia south to Florida, west Illinois, Arkansas and Texas.

Two small-leaved Tertiary species of *Ulmus* have been described. Both differ significantly from the Thorn Creek species. *U. Moorei* Chaney & Elias differs in having almost orbicular leaves with a broadly cuneate or somewhat cordate nearly symmetric base, fewer secondaries and a thicker texture. The leaves of *U. Brownelli* Lesq. are widest below the middle, with teeth abruptly narrowed to form a sharp tip, pointing outward in the basal portion and upward in the apical portion.

U. Tanneri Chaney from Eagle Creek, Oregon, shows the greatest likeness to the Thorn Creek leaves. It is however, based upon leaves that are less unequal at the base with more prominent accessory teeth and a more obtuse apex.

Only the two faces of a single specimen of an elm fruit have been found. Among living species this fruit appears to be practically identical

with the winged fruits of *U. racemosa* Thomas. The cork elm is widely distributed in north-central United States from New York to Nebraska and from southern Ontario to central Tennessee. It usually grows on dry gravelly uplands, along river cliffs or on rocky slopes.

It is quite possible that this fruit belongs to *U. paucidentata*, but no certain assignment to that species can be made until the leaves and fruits have been found more than once in association, or until sufficient collecting has been done to give reasonable assurance that the florula had only one elm species.

Magnolia oregoniana Chaney

Magnolia oregoniana Chaney, Contr. Walker Mus. 2, no. 5: 173, pl. 15, fig. 1, 1920.

Leaf coriaceous, ovate-elliptic, about 7 cm. long, 3 cm. wide, margin entire, base round-cuneate, uneven. Except for its somewhat smaller size this single specimen is like that figured by Chaney from Eagle Creek. Its nearest living equivalent would seem to be *Magnolia virginiana* L. The sweet bay or swamp laurel occurs from Massachusetts and Long Island southward in the coastal plain to Texas. In habit it may be a small tree, but in its northern range it usually occurs as a shrub. As suggested by its common name, it usually grows in swampy places, being found along the borders of pine-barren ponds and in shallow swamps.

Celastrus (?) sp.

This genus is somewhat doubtfully represented by a single specimen of a three valved fruit. It bears a striking resemblance to the fruits of *C. scandens* L. Since no leaves referable to this genus have as yet been found, a description of the species is withheld.

Celastrus scandens is found throughout the eastern United States and extends as far west as New Mexico. The other species in the genus are found principally in the mountainous regions of India and China and extend to Japan, Malaya and Australia.

Rhododendron idahoensis n. sp.

Plate 13, figs. 6, 10

Leaf narrowly oblong, narrowing in the upper fourth to the acute apex and more abruptly in the basal region to the cuneate, slightly uneven base; length of best preserved specimen 5.8 cm., width 1.6 cm., width of others

up to 2.7 cm., length unknown; margin entire, slightly undulate; midrib stout, crooked; secondaries about 15 pairs, forking well within the margin to form loops with the forks from adjacent secondaries, secondaries not parallel, arising irregularly at angles of 45–65°; no tertiary venation; ultimate venation a fine obscure reticulum; surface on some specimens punctate; petiole stout, length unknown but at least .5 cm. Type, Mus. Paleon., Univ. Mich., no. 20018.

The character of the obscure venation is very similar to that of *Rhododendron maximum* L., the great laurel of the northeastern United States and Appalachian region. The fossil leaves are much smaller and thinner. *R. maximum* is a tree-like shrub that often forms large almost impenetrable thickets along streams and in wet ground in the southern Appalachians. It ranges up to about 4000 feet elevation.

Fraxinus sp.

Several small samaras with obscure seeds were found. Except for their smaller size they resemble those of *F. quadrangulata* Michx. The latter is found in rich woods from Ontario to Michigan and Minnesota and to Alabama and Arkansas. No leaf impressions referable to *Fraxinus* have as yet been found in the Thorn Creek locality.

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Peat Formation in the Carolina Bays

MURRAY F. BUELL

(WITH ONE FIGURE)

On the coastal plain of North and South Carolina there are a large number of shallow, elliptical depressions, the long axis of each of them being oriented south approximately forty-six degrees east. These are commonly known as the Carolina Bays. Melton and Schriever (1933) described them and suggested a meteorite origin. Further evidence substantiating this hypothesis has been accumulated by Prouty (1935) in his magnetometer surveys. All the phenomena described by these men seem to be adequately explained only by the meteorite hypothesis. Two dissenting interpretations, however, have been presented. C. Wythe Cooke (1934) has ascribed their origin to wind action and water currents in coastal lagoons. Douglas Johnson (1937), on the other hand, has proposed an hypothesis of complex origin which involves artesian, solution, lacustrine, and aeolian factors.

The time and mode of origin is of considerable importance in any study of their subsequent history. If they were formed by a meteorite shower they are identical in age. If, then, the Pamlico terrace can be correlated with either the Peorian interglacial or the mid-Wisconsin as Cooke (1930, 1935) suggests, then the bays were formed in late Pleistocene time since only those on the Pamlico terrace are interfered with by beach ridges. Since their formation some of them have doubtless been obliterated through erosion. Some have been modified through drainage and are more or less completely under cultivation. A few contain lakes. The majority, however, are completely filled with peat.

A study of the historical record of the peat deposits will doubtless cast considerable light upon post glacial history in this area. Preliminary studies in Bladen County, North Carolina, give no indication that the bays this far inland had a marine origin or have since been invaded by the ocean as have those peat areas on the Pamlico terrace (Dachnowski-Stokes and Wells, 1929; Cocke, 1934). Pollen is abundant in most of the horizons. When a study of the pollen spectrum is completed its correlation with results of similar studies in northern bogs will prove to be of considerable value. The present paper, however, deals only with the method of peat formation as it is illustrated in the few lakes still in existence in these depressions.

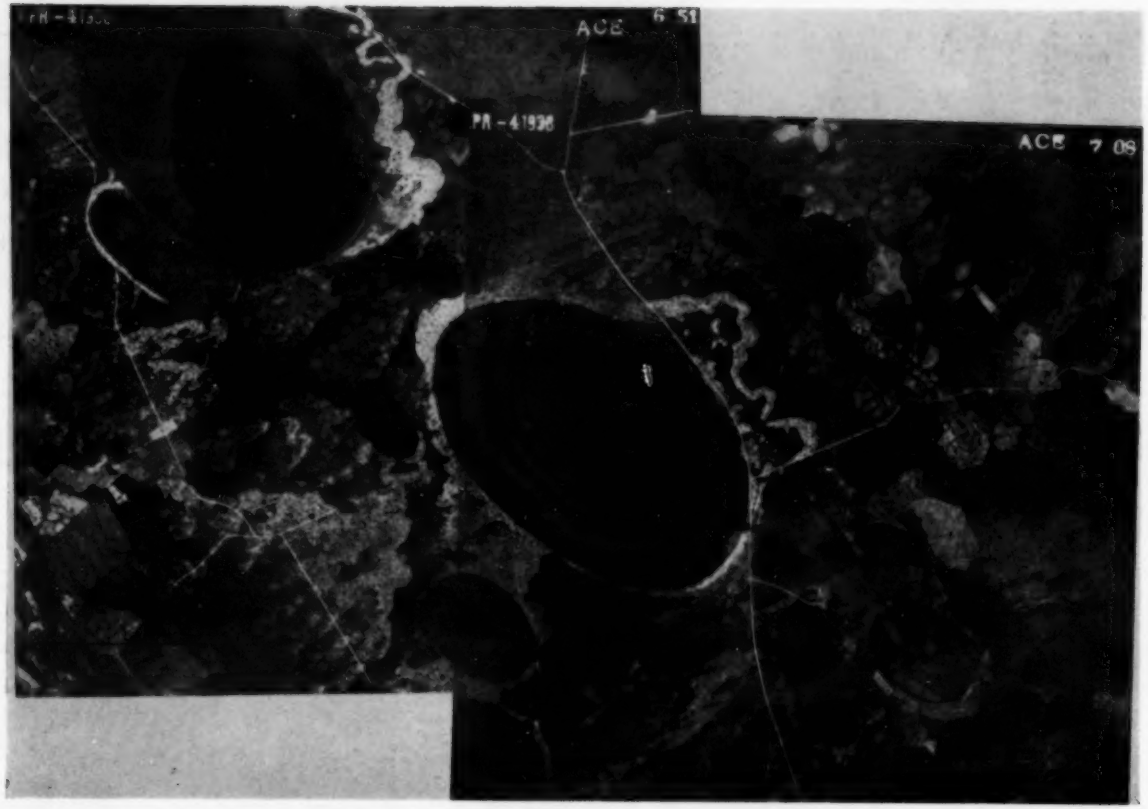

Fig. 1. Aerial photographs of a portion of Bladen County, N. C., showing Salter Lake, upper left, and Jones Lake, center. The dunes associated with these lakes lie on the east side of their basins. Several smaller "bays" filled with peat are shown. Southeast of Jones Lake are some "bays" which have been drained and are under cultivation. (*Photo by Agricultural Adjustment Administration.*)

During the course of the study of Jerome Bay, a peat deposit in Bladen County, North Carolina, it became evident that this is a filled-in lake basin. The pattern of vegetation suggested that the lake had filled in most rapidly from the north and the west sides, very slowly from the south and the east sides. Recent aerial photographs of this part of the State, which have been supplied by the Agricultural Adjustment Administration, furnish evidence that this has probably been the case. Of the several lakes which still exist in such depressions all occupy the southeast portions of their original basins. The north and west portions of the lake basins have been more or less filled in with peat.

Two features are responsible for this pattern of peat deposition. One is the direction of the prevailing winds. The second is the shape of the basins, the bottom profiles of which give promise of being constant for all the bays.

The prevailing southwest winds have favored peat deposition on the west, while slowing up the process on the east side of the lakes. That the prevailing winds have been from the southwest since the formation of the depressions is evidenced in the dunes, now stabilized, which were blown out from the sand rim at the southeast end before revegetation occurred. The winds, by accentuating wave action on the east side of the lake, greatly retard the rate of marginal encroachment and inhibit island formation about cypress bases and knees. On the lee side, quiet water prevails, and the undisturbed condition is reflected in the character of the vegetation which is vigorously invading the lake.

The second factor affecting the peat deposition in these lakes is the character of the lake basins themselves. The bottom profile along the long axis is known fairly accurately for Jerome Bay. A long, deep basin occupies the central and southern portions while at the north end there is a broad, gently sloping shelf. The deepest point, 11 feet, is at the center. South of this the deep basin extends 2000 feet, its profile rising gradually to a five foot depth 500 feet from the south end. There is then a rapid rise from this 5 foot depth to the sand rim at the south end. North of the center the basin continues deep for 500 feet but in the second 500 feet it rises rapidly to a 5 foot depth. Thence is a long gradual slope about 1500 feet northward across the broad shelf at the north end. Soundings in two nearby lakes, Jones and Salter Lakes, as well as in the surrounding peat indicate similar profiles.

That peat accumulation should be more rapid from the north end would be expected, considering the method by which peat is formed in

these southern lakes. The principal pioneer is the pond cypress, *Taxodium ascendens* Brong., which becomes established on the exposed lake bottom during the dry seasons when the water is low. Obviously over a broad shallow slope, such as is characteristic of the north ends of these depressions, broader expanses of bottom are exposed during drouths than where the bottom dips more steeply. Once the cypresses are established their buttressed bases and knees become nuclei for islands of shrubs and trees. The most common of the pioneer shrubs are *Pieris nitida* B. & H., *Cyrilla racemiflora* Walt. and *Clethra alnifolia* L. along with which a few trees, primarily *Persea pubescens* (Pursh) Sarg., *Acer rubrum* L. and *Chamaecyparis thyoides* (L.) BSP. become established. In addition to the island development about the cypress trees, there is a mass advance of the vegetation into the lake from the margin, the same species predominating. This marginal encroachment as well as the growth of the islands is accomplished through the stoloniferous habit of some of the shrubs together with the spreading superficial root systems of all the woody bog plants. A dense, strong mat is thus formed which grows out into the water. The growth of this mat is slow and it never extends more than a few feet beyond the completely peat-filled portion of the lake. Under the narrow, free outer portion of the shrub mat the gradient of the mucky lake bed is often very steep so that there may be as much as three feet of water below its edge at normal water level. A very large amount of filling in of the lake is by the wash of fine materials toward the center from this overhanging marginal mat as well as from the islands. Frequent outward drift of logs and fallen trees and their subsequent sinking to the oozy bottom adds considerably to the accumulation. Mat development dependent upon the completion of this filling in is naturally more rapid over shallower portions of the lake.

In contrast with the conditions prevailing in most northern bog lakes, in these lakes there is almost no herbaceous aquatic vegetation. In this climate pronounced fluctuation of lakes together with hard sandy bottoms may be the factors inhibiting the growth of marsh plants. Or it may possibly be the excessive staining of the water as suggested by Martin and Uhler (1939). Furthermore herbaceous plants, rather than being of primary importance in mat formation, are very scarce among the shrubs and trees that form the bog mat. The most prominent difference of all is the pioneer rôle taken by aquatic trees in the advance of the

vegetation into the lakes. This is a situation extremely different from the retarded position of trees in the aquatic plant succession in the north.

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Some New Myxophyceae from Southern California

GEORGE J. HOLLENBERG

(WITH EIGHT FIGURES)

Algal collections in southern California during the past several years have yielded a number of Myxophyceae of considerable interest, some of which are apparently new. Several of these are described herewith.

Myxohyella seriata sp. nov. (Fig. 1)

Plants filamentous, totally endophytic; filaments simple or sometimes dichotomously branched below, 100–140–(170)μ long; young plants and deeper portions of older plants composed of a single row of cells 3–6μ diam. and 15–30–(40)μ long; distal portion of filaments gradually larger, up to 12μ diam., the cells dividing in three planes to form a number of tiers of 4–8–(16) small cells (endospores) 2–3μ diam.; protoplasm finely and uniformly granular, very pale blue-green; sheath thin and hyaline; filaments abundant, penetrating deeply between the filaments of a species of *Isactis*.

Plantae totae endophyticae; filamentis simplicibus aut nonnullis dichotomo furcatis, 100–140–(170)μ longis; partibus profundibus ex una serie cellularum 3–6μ latis et 15–30–(40)μ longis constitutis; partibus superioribus gradatim majoribus, vel 12μ latis; nonnullam seriem stratorum ex 4–8–(16) cellulis (endosporis) parvis 2–3μ latis compositorum formantibus; protoplasma subtiliter granulosum, pallide aerugineum; vaginis tenuibus hyalinis. Hab. In *Isactis* sp.

This plant was first collected in the fall of 1934 from above high tide level at San Pedro in Los Angeles County. Later it was found abundant on spray covered rocks above high tide level near Corona del Mar in Orange County. At both of these stations it has been collected a number of times at different seasons of the year. More recently it has been collected near high tide level on the bay side of Punta Banda, Lower California, Mexico. It appears to be perennial and seems to be a common endophyte in a species of *Isactis* to which it appears to be limited. A number of specimens of *Isactis* from the Pacific Coast in the herbarium of the University of California appear to be identical with the host of *Myxohyella seriata*. Most of them were collected from the central and northern part of the state. The endophyte was not found in any of them. It seems likely, therefore, that it is a plant of warmer coasts.

Soon after the filaments become established in the host, the cells at the outer end gradually increase in size, beginning at the outermost cell. Spore formation is initiated by a longitudinal division of the outermost

cells. This division may be preceded by a transverse division. A second longitudinal division generally occurs at right angles to the first and is followed by a tranverse division. There is usually another division in an irregularly oriented plane. As a result 16–32 small cells are usually formed by division of a single cell of the filament. These apparently represent endospores which are liberated by disintegration of the parent cell wall as new ones are continuously formed by transformation of successive cells of the filament.

This plant seems amply distinct from all other species of *Myxohyella*. The very elongate cells of the deeper portions and the more or less regular divisions of the upper cells into tiers of 8–16 cells seem most distinctive features. The plant is also considerably larger than previously described members of the genus. Of the several collections made by the writer number 2379B is considered the type. It was collected from the top of a small municipal concrete breakwater at Cabrillo Beach, San Pedro, in Los Angeles County, October 22, 1938.

Entophysalis marginalis sp. nov. (figs. 3–5)

Colonies irregularly lobed, 1–3 mm. diam., firm, cartilaginous and light yellow in color; inner cells of the colony spherical or slightly oval, 2.5–3.5μ diam., mostly in pairs with a hyaline sheath, widely separated in a firm hyaline matrix, and more or less arranged in rows which radiate toward the surface of the colony; outermost cells 7–8.5μ diam.; protoplasm finely granular, pale blue-green.

Coloniae irregulariter lobatae, 1–3 mm. crassae, firmae et cartilaginosae; color diluto-flavae; cellulis interioribus globosis aut leviter ovatis, 2.5–3.5μ diam., plerumque in paribus cum vaginis hyalinis, in matrice hyalina gelatinoso-firma late separatis, plus aut minus in ordinibus dispositis, qui ad superficiem radiant; cellulis majoribus et ordinibus plus explicatis ad superficiem coloniae; cellulis extimis 7–8.5μ diam.; protoplasma tenui-granulosum, pallide aeruginosum. Hab. ad saxa praehensae.

The type material, number 1562A, was collected by the writer in October of 1936 on the leeward side of a small concrete municipal breakwater at Cabrillo Beach, San Pedro, Los Angeles County. Numerous colonies were present, covering an area a foot or more across. Sheaths around cell groups are more distinct at the surface of the colony. As a result the surface view of the colony resembles a *Gloeocapsa* (fig. 5). The sheaths and matrix near the surface of the colony are yellowish in color. Larger granules are occasionally present in the finely granular protoplasm. The close crowding and compressed shape of the superficial

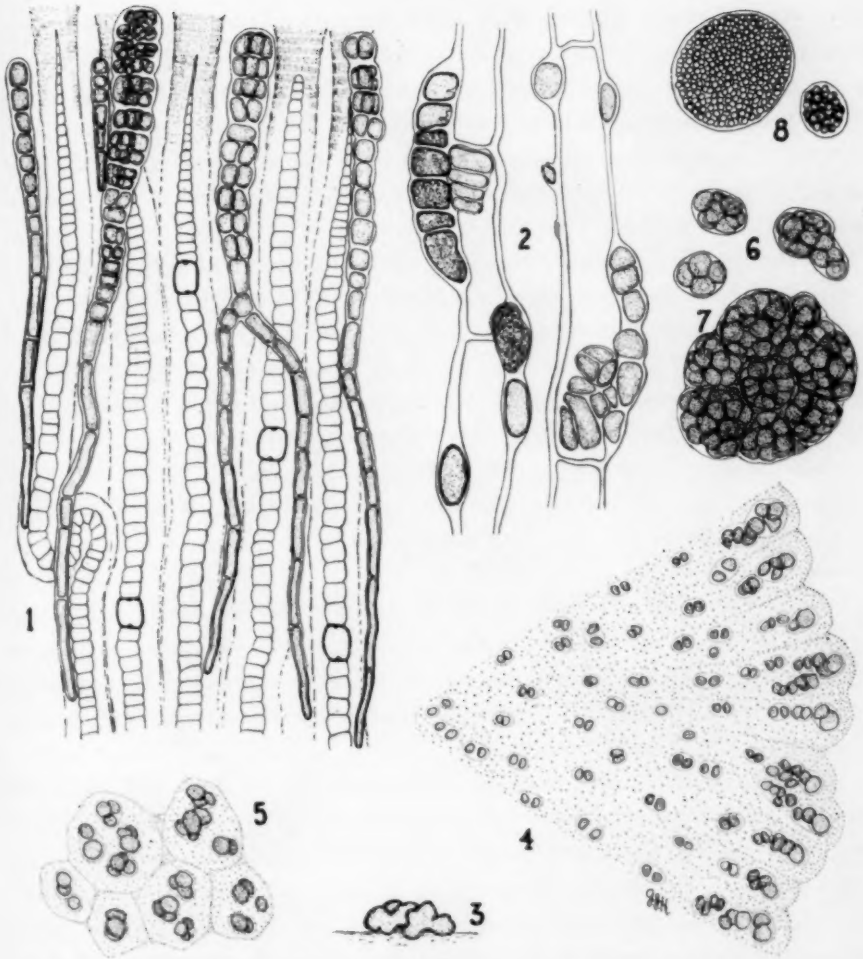

Fig. 1. Several plants of *Myxohyella seriata* sp. nov. among the filaments of the host, showing endospores forming at the outer end. ×700.

Fig. 2. *Xenococcus pulcher* sp. nov. in the walls of a species of *Chaetomorpha*, showing young stages becoming embedded in the wall of the host, mature plants, and endosporangia with endospores. ×325.

Fig. 3. Habit sketch of *Entophysalis marginalis* sp. nov. ×2.5.

Fig. 4. Thallus structure of *Entophysalis marginalis* in radial view. ×325.

Fig. 5. Surface view of a portion of a colony of *Entophysalis marginalis*. ×325.

Fig. 6. Young colonies of *Microcystis splendens* sp. nov. ×700.

Fig. 7. Older colony of *Microcystis splendens*, showing the formation of subcolonies. ×700.

Fig. 8. Colonies of *Microcystis ovalis* sp. nov. ×700.

cells suggests that they are more actively dividing than the more widely separated inner cells. The progressive decrease in size of the cells from

the surface toward the center of the colony also indicates that cell division is largely limited to the outer cells of the colony. In fact the outermost cell of each radiating row appears to function as a kind of apical cell, primarily responsible for the increase in the diameter of the colony. Frequent more or less anticlinal divisions of these outermost cells result in the gloeocapsoid superficial aspect. Cell division was the only type of reproduction observed.

The genus *Entophysalis* was for some time considered only imperfectly distinguished from *Gloeocapsa*. Gardner (1927) in discussing the genus emphasizes the importance of the fact that cell division is largely limited to one plane in *Entophysalis*. The plant here described is further distinguished by the fact that cell division is largely limited to the cells at or near the surface of the colony. *Entophysalis marginalis* is closely related to *E. granulosa* Kuetzing, the type species. A bit of the type material of *E. granulosa* has been sent to the herbarium of the University of California from the Kuetzing herbarium. A fragment of this material was examined by the writer. In *E. granulosa* the cells of the colony are nearly of the same size throughout the colony and cell division does not appear to be at all limited to the superficial cells of the colony as in *E. marginalis*. The inner cells are not so widely separated in *E. granulosa* nor are they as distinctly in pairs but the inner cells are more distinctly in rows than in *E. marginalis*.

Gardner (1927) expressed doubt concerning the presence of *Entophysalis* in this country, although an undetermined species, number 99786 in the herbarium of the University of California, was collected from rocks at high tide level at Carmel Bay in central California, presumably by either Setchell or Gardner. The latter plant resembles the southern California plant somewhat but seems nearer to *E. granulosa* in most respects, especially in the nearly uniform diameter and distribution of the cells.

Xenococcus pulcher sp. nov. (fig. 2)

Plants endophytic, solitary or aggregated, up to 25μ diam., more or less flattened, dividing in two planes only; protoplasm finely granular, distinctly reddish; endosporangia 15–20–(30)μ broad, forming numerous endospores 2–2.5μ diam. and likewise reddish in color.

Plantae endophyticae, solitariae aut aggregatae, vel 25μ latae, plus aut minus compressae, in duobus planis solum dividentes; protoplasma subtiliter granulosa sensim rubra; endosporangiis 15–20–(30)μ latis, endosporas numerosas 2–2.5μ latas formantibus. Hab. In muris *Chaetomorphae* sp.

This striking plant was found as an abundant endophyte in the walls of a minute plant which is probably an undescribed species of *Chaetomorpha*. The latter was attached to piling near low tide level on the bay side of the government breakwater at Cabrillo Beach, San Pedro, California. In habit it resembles *X. endophytica* described by Setchell and Gardner (1937) from the Galapagos Islands. It occurs in a different host but the host is often more or less distorted by the growth of the endophyte as in the case of *X. endophytica*. The plant here described differs from *X. endophytica* in the distinctly larger size of the cells and in the pronounced reddish color of all cells. The cells are mostly lenticular-compressed. They appear to possess a thin wall of their own, hardly distinguishable from the wall of the host in which they are imbedded. The plant was first collected in October of 1936. Number 2145 in the herbarium of the writer was collected a year later at the same place. It is considered the type material.

Microcystis splendens sp. nov. (figs. 6, 7)

Colonies spherical to irregular, commonly 20–50μ diam. but frequently up to 100 or even 170μ, the larger colonies often composed of subcolonies; colonial tegument thin and hyaline; cells closely packed, spherical or angular by mutual compression, 3.5–5μ diam.; protoplast brilliant blue-green, uniformly granular and without pseudovacuoles.

Coloniae sphericae aut irregulares, plurimum 20–50μ, sed saepe 100 aut 170μ crassae; coloniae majores saepe ex subcolonis constitutis; tegumentis colonarum tenuibus et hyalinis; cellulis globosis aut plerumque per pressuram angulatis, 3.5–5μ crassis; protoplasma tenui-granulosum, splendido-aeruginosum.

The brilliant blue-green color seems distinctive. Colonies break up and start new colonies, separating readily with a slight pressure on the cover glass. Application of a solution of methylene blue shows the absence of a sheath around the individual cells when so separated, although narrow colorless sheaths are quite evident around even very small colonies. This interesting plant has appeared several times in old culture dishes of germlings of brown algae in the laboratory at La Verne College, frequently in company with *M. ovalis* of this paper. In the cultures the colonies were attached to the glass slides and eventually became very abundant in the culture dishes. Type material Hollenberg number 2179C.

Microcystis ovalis sp. nov. (fig. 8)

Colonies simple, spherical or commonly oval and smooth in outline, with distinct hyaline tegument; cells closely packed, spherical, 1.5–2μ diam.; pro-

toplast pale blue-green or slighly olivaceous, without pseudovacuoles or conspicuous granules.

Coloniae simplices, globosae aut plerumque ovatae et leves, cum tegumentis distinctis et hyalinis; cellulis globosis 1.5–2μ crassis, confertim compressis; protoplasma pallidum et plus aut minus luteolum aeruginosum, sine granulis conspicuis.

Microcystis ovalis has been encountered several times in old cultures of germlings of marine algae kept in the laboratory at La Verne College, La Verne, Cailfornia. The plants multiplied rapidly in the culture dishes throughout the summer and fall of 1938. The cells appear to be smaller than those of previously described marine members of the genus. Type material, Hollenberg number 2179D.

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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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